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PROCEEDINGS
OF
THE LINNEAN SOCIETY OF LONDON



145TH SESSION

FROM OCTOBER 1932 TO MAY 1933

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THE LINNEAN SOCIETY OF LONDON

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PROCEEDINGS
OF
THE LINNEAN SOCIETY OF LONDON

(ONE HUNDRED AND FORTY-FIFTH SESSION,
1932-1933)

COMMEMORATION OF THE CENTENARY OF THE BIRTH OF
JULIUS VON SACHS

20 OCTOBER 1932

Professor F. E. WEISS, F.R.S., President,
in the Chair

The PRESIDENT referred to the effort he had made to collect from Fellows of the Society the necessary sum for the purchase of the portrait of Julius von Sachs, painted by his daughter, Maria Sachs. He had been successful in enlisting sufficient support for the proposal, and on behalf of the subscribers he had offered the portrait to the Council, which had accepted the gift. It remained therefore for him to hand the portrait over to the Society, which he had great pleasure in doing.

The President then continued :

‘It seems fitting to devote part of our proceedings this evening to a commemoration of the centenary of Sachs’s birth. Actually his birthday was on the 2nd of October, on which day a centenary celebration was held in Würzburg, where Sachs had held the Professorship of Botany for nearly thirty years.

‘Sachs’s name and work will not be so familiar to the younger botanists as to those of us who studied botany in the latter half of the 19th century, and who were brought up on Sachs’s great Textbook of Botany. While eminent as a plant physiologist, he had a wide general outlook on botany, and was the author of the best ‘History of Botany’ that we have. But above all he was pre-eminent as a teacher, and attracted

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students from all countries. Marshall Ward, Francis Darwin, and Walter Gardiner were among his pupils, and we are favoured this evening by the presence of two of his most distinguished pupils, Dr. D. H. Scott and Professor F. O. Bower who have both come considerable distances to take part in our commemoration of Sachs's services to Botany. We greatly appreciate their presence and are most grateful to them for agreeing to take part in our proceedings to-day. But before calling upon them to speak I will read a communication which I have received from one of our former presidents, Dr. S. H. Vines, who is unfortunately unable to be present owing to ill-health. He, too, was a student in Sachs's laboratory in Würzburg.'

Professor S. H. VINES, F.R.S.: It is a matter of great satisfaction to me that the Linnean Society should not have allowed the centenary of one of its most distinguished Foreign Members, Julius von Sachs, to pass unhonoured. To my great regret the state of my health prevents me from being personally present on this occasion. But my regret is mitigated by the kindness of the President, who has invited me to send to him in writing what I should have preferred to say *vivâ voce*. My only qualification to take so prominent a part in these proceedings is the fact that, many years ago, I was for a short time one of Sachs's pupils, and that he admitted me to the privilege of his friendship.

It is, no doubt, pertinent to enquire what are the reasons which move us to offer this our tribute of admiration and esteem to Sachs's memory. I cannot but think that if this question were put generally to botanical students the predominant answer would be his greatness as a plant-physiologist. That answer would be quite satisfactory, so far as it goes. It was in this department of botanical science that he made his researches and attained results of the first importance. But great as are his merits in this direction, I would venture to urge that his most effective contribution to the advance of the science was his 'Lehrbuch der Botanik', which has influenced and stimulated the studies of botanists in all parts of the world.

This proposition may perhaps cause some surprise. It prompts the cynical criticism 'Anybody can write a text-book'. Quite true: it is being done frequently. But it takes *somebody* to write a text-book of the calibre of Sachs's 'Lehrbuch'. The complete mastery of his matter which the book reveals proves that he was not only a great physiologist but also a great botanist. The main branches of the science are treated with sufficient fulness to bring the essentials of them within the grasp of the student, in a lucid logical style which is intellectually satisfying. Moreover, the text

is documented by references to the great men of the past by whose labours and writings the *corpus* of botanical knowledge has been built up. But all these purely material good qualities would have availed but little had they not been quickened into life by the inspiration of genius, without which the book would never have been accepted as a revelation, nor would it have led on to a revolution in the teaching and study of botany.

In explanation, I would briefly sketch the history of the science in the period immediately preceding the publication of the 'Lehrbuch'. It may be stated with sufficient accuracy that during the first half of the nineteenth century taxonomy was still the dominant botanical study, to the almost complete exclusion of the other branches of the science. The first overt revolt against this tyranny was the publication, in 1843, of Schleiden's 'Grundzüge der wissenschaftlichen Botanik'. This was a real live book, full of all the available knowledge in the various branches of the science, which appealed to the reader by the vividness of its style and by the caustic criticisms which were scattered through its pages. But this text-book, with all its merits, though it certainly stirred the dry bones, does not appear to have had any permanent effect on the teaching of botany in Germany or elsewhere. It is, however, worthy of note that its publication coincided with the foundation of two 'modernist' periodicals, the 'Botanische Zeitung' (Mohl and Schlechtendal, 1843) and the 'Zeitschrift für wissenschaftliche Botanik' (Schleiden and Naegeli, 1844). The book was published in English in 1849, with the effect that Professor Arthur Henfrey was inspired to establish teaching on these lines at King's College, which might have succeeded had not his life been prematurely cut short in 1859.

So the teaching of botany remained in the old grooves until the appearance of Sachs's 'Lehrbuch' in 1868. It is not improbable that Sachs was stimulated to this great effort by his high opinion of Schleiden and of his book, which had now fallen behind the times. Schleiden's 'Grundzüge' and Sachs's 'Lehrbuch' are books of the same class, having this in common, that they are really living: but the 'Lehrbuch' is the more coherent and convincing. It was received everywhere with acclamation. New editions were called for at short intervals (1870, 1873, 1874); and it was translated into French and into English. Its effects on botanical teaching soon became more and more apparent: the revolt against the hegemony of systematic botany was this time completely successful. I will illustrate this with an account of its effect upon the teaching of botany in this country. When I began to study botany, in 1870, the pursuit of systematic botany was at its zenith in England, which was, in fact leading the

world. With such masters at work as Joseph Hooker, Bentham, Daniel Oliver, and J. G. Baker the issue of Floras of the British Colonies and Dependencies was almost continuous, and the great 'Genera Plantarum' was already well advanced. On the other hand, the teaching of botany was quite inadequate. Botany was taught not for its own sake, but as a compulsory part of the medical curriculum. The teaching, which was confined to the summer term, was purely taxonomic and quite elementary in character. The Natural Orders enumerated in the medical syllabus were gone through with the help of a more or less adequate supply of specimens. The morphology and anatomy of plants were discussed only in so far as they were related to the characteristics of the Natural Orders, providing the technical vocabulary required for the formal description of plants. Physiology was hardly mentioned at all. In a word botany was not taught as a biological science. Had it not been relegated once for all to the category of the 'Classificatory Sciences' by the great Whewell in his 'History of the Inductive Sciences'? As a striking example of the low estimation in which it was generally held I may mention the fact, from my own personal experience, that as late as 1873, botany was not included as a subject in the final examination for the degree of B.Sc. of the University of London.

When the ferment of Sachs's 'Lehrbuch' began to work in England, it aroused the enthusiasm of a young botanical professor, W. T. Thiselton Dyer (afterwards Sir W. T. Thiselton-Dyer, Director of Kew), who began teaching on the lines of the 'Lehrbuch', and brought it into prominence by courses of lectures, with practical work (including microscopy), at the Royal College of Science, South Kensington (1874-6). This innovation at once captured public attention, for hitherto the botanical student had not been provided with either laboratory or microscope. Professor Dyer put the coping-stone to his work by preparing a translation of the 'Lehrbuch' (Ed. 3), which was published by the Clarendon Press in 1875. Botany, whole and undivided, was now taught as a biological science for its own sake, and took its rightful place in the scientific curriculum of every university. Laboratories were created all over the land, not only in universities and colleges, but also in schools, so that almost any schoolboy has to-day at his disposal facilities for study which were not available for anyone in 1870.

Of course this rather sudden and violent biological reaction excited the criticism of the established systematic teachers. They spoke contemptuously of the modern methods as 'the New Botany', but quite illogically; for it was not a 'New' Botany at all—it was the revival of the old British Botany,

created by Grew, Malpighi, Hooke, Ingenhousz, Knight, Robert Brown, which had been allowed to fall into desuetude. But they soon realized the position, and made co-operative terms with the innovators. Nor did systematic botany suffer by the change. Since those days it has made some notable advances which could only be achieved by knowledge gained by the biological methods of investigation, and it is now better taught than ever before.

I do not know if you will consider that I have made out a case for my proposition concerning the relative significance of Sachs's achievements as researcher and as teacher; but I hope that I have at least made it clear that, from either point of view, we have ample reason for commemorating the life and work of Julius von Sachs.

Dr. D. H. SCOTT, F.R.S., said :

'My personal knowledge of Sachs dates from the years 1880-2, when he was just at the zenith of his work and fame. It was in 1882 that he published his "Vorlesungen über Pflanzen-Physiologie", the last of his great books. I went to Würzburg by the advice of Thiselton-Dyer, supported by Vines. At that time our inspiration as botanists came from Germany, and any one who wished to study the science seriously was expected to go and work there.

'On arriving I called on Sachs at his house. He asked me where I was staying, and said: "Tell the landlord that you are working with me; then he will know that he has to be civil"—a trivial remark, but quite characteristic of Sachs.

'Next morning I started work in the laboratory. There were no students in the ordinary sense, only a very select few, just one or two, who intended to become botanists. We therefore had much personal attention from the professor, who directed the work in detail, of course with the help of his brilliant assistant Goebel. The ordinary students, chiefly medical, only attended the lectures, and very rarely were given a demonstration in the laboratory, to the annoyance of the regular workers.

'Sachs's lectures were brilliant—the finest I ever heard—comparable, I am told, to those of Huxley. Sachs had great artistic gifts; not content with the blackboard, he would, on special occasions, make an elaborate coloured drawing on cartridge-paper before the eyes of the class.

'These were the elementary lectures. When the summer term arrived Sachs started special physiological lectures on Saturdays. These, with the experiments shown, lasted $1\frac{3}{4}$ hours, while the ordinary lectures were limited to three-quarters of an hour. Although I never became a physiologist, it was a great experience to witness the experiments and hear

the exposition of the leading plant-physiologist of his day. Sachs's remarks were often humorous, both in lectures and conversation. Once he was speaking of insectivorous plants, and dealt with the objection that they can live without any animal food. "In Poland and Ireland", he said, "a great many people live only on potatoes, but it does not follow that a beef-steak would'n't be a good deal better".

'For the first four or five months I was going through a general course of microscopic botany, and a very good course it was. After that I was advised to work for the Ph.D. degree, and then my special subject of research was the development of the articulated milk-vessels. The approval of the resulting dissertation by Sachs was the chief condition of obtaining the degree, but there was also a *viva voce* examination in Botany, and, as subsidiary subjects, in physics and chemistry.

'From my first day in the laboratory I had to make drawings of what I saw. "What one has not drawn one has not seen" was a great principle of Sachs's.

'Within the last few days a full biography of Sachs has appeared by Prof. Ernst Pringsheim of Prag. It is a most valuable treatise on the life and work of the great botanist. The author lays much stress on Sachs's influence in England, and specially mentions our celebration here to-night and the purchase of the portrait now presented. He says: "One sees from this how faithfully his English admirers still, to this day, think of their teacher". One little point in the biography may also be worth mentioning. We are told how Sachs, when quite a boy, was attracted by an article in the English "Penny Magazine" on the great fossil reptiles. Few will now remember that excellent publication, as I do. It is interesting to think that an English popular journal had some share in winning Sachs's attention to natural history.

'The portrait which we welcome to-night was first brought to our attention in a letter to me from Prof. Goebel. It is sad, indeed, that within the last few days this distinguished man, himself a leading figure in our science, has passed away, as has also the artist, Sachs's gifted daughter.

'Sachs was not only a great physiologist, he was also unsurpassed as an all-round botanist, the author of the greatest text-book of the subject, master of all its branches! Hence his vast influence, nowhere stronger than in our own country.'

Professor F. O. BOWER, F.R.S., said :

'As the ground has been fairly covered by what has gone before I shall centralize my remarks on the young student of botany of the seventies in one of our own universities.

who found it necessary to attend a German university to acquire the point of view and laboratory methods there adopted and practised. Great Britain, though then pre-eminent in systematic botany, had in the sixties and seventies neglected in its universities that general advance in the practical study of the science which had been made in the continental schools, particularly in Germany. The key to this was already provided for us by the English version of the Text-book of Sachs, edited by Thiselton-Dyer, and published in 1875. We who had greedily absorbed its pages, but without the necessary facilities for verification by practical work at home, longed to reach the fountain head. The most direct way was to enter a German university as a student. In 1877 Professor Vines, already a Fellow and Lecturer at Cambridge, suggested to me to join him at Würzburg under Sachs himself. I was already conversant with simple microscopic methods, but on entering Sachs's laboratory I was taken directly in hand by the Master himself, and introduced not only to the technique of preparation according to the Hofmeisterian methods, but, what was still more valuable, to the methods of observation and delineation, in which Sachs himself excelled. I believe his father was a woodcut artist—certainly Sachs was a splendid draftsman, as witnessed by the illustrations in his Text-book. Doubtless they were drawn by him on the wood-blocks. I remember particularly his cryptic utterance that "every drawing conveys a view". Without any departure from accurate delineation the artist expresses what he understands himself to have seen, with the result that his personality is inseparable from the drawing, just as the personality of Sachs still speaks to us not only from the text, but also from the illustrations of his classic volume.

'I was one of a stream of English students who visited Würzburg: for instance, Sir Francis Darwin, Vines, Scott, Marshall Ward, and Gardiner. All were impressed by the personality of Sachs. He was a splendid exponent of his science; while at the back of what he said or wrote one detected the outlook of the true philosopher. The portrait before us was painted long after 1877, when he was 45 years old and in the full plenitude of his powers. It hardly conveys to me the almost ethereal expression of the finely chiselled face—it probably reflects some of the troubles of a later time; but none the less, it will perpetuate on our walls a personality to whom British Botany owes much.'

GENERAL MEETINGS

27 OCTOBER 1932

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the Anniversary Meeting held on Thursday the 24th May 1932, having been circulated, were taken as read and confirmed.

The PRESIDENT reported the deaths of the following members of the Society :—William Francis, Leonard Goodhart Sutton, Dr. John Mastin, Dr. Malcolm Laurie, Thomas Parkin, and James Walter White, Fellows; Herbert C. Chadwick, Associate; and Professor Karl Ritter von Goebel, Foreign Member.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—John Guy Dollman and The Right Hon. The Earl of Cranbrook.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Mohamed Eweis; for the first time, in favour of William Charles Osman Hill, Abbas Fathi el-Helaly, John Hugh Davie, Chrystabel Prudence Goldsmith Procter, John Vardy, Reginald Edward Vaughan, and Harold Alexander Wootton.

Mr. W. C. WORSDELL, A.L.S., exhibited abnormal specimens of *Papaver nudicaule* L. from the gardens of Gen. J. S. Gallie, Church Oakley, Hants, and Mr. R. J. Flintoff, Goathland, Yorks.

In both specimens the normal calyx has become persistent, much larger, and displaced a shorter or longer distance down the flowering stem. In compensation, a new calyx is being formed by transformation, complete or partial, of petals into sepals to the number of two or three. At the same time new petals are being supplied by transformation of stamens. In the extreme cases the displaced normal sepals occupy the position of *bracts* such as occur in most other species of *Papaver*, but not in *P. nudicaule* (hence the name).

The fact that the new sepals derived from the petals are exactly similar to the displaced normal ones supports the view that the latter have also been derived from *petals* and not from *bracts*. The displacement of the normal sepals can have only one meaning, viz., that it represents a reversion to the condition obtaining in other species in which *bracts* are always

present. If that is so, then it follows that the *bracts* in *Papaver* have been derived from the *calyx* and not from foliage-leaves.

Dr. D. H. SCOTT said that it was remarkable that the same anomaly had turned up, in the same season, at Oakley in Hampshire and in Yorkshire. He recommended everybody who came across such monstrosities to send them to Mr. Worsdell.

The PRESIDENT, thanking Mr. Worsdell for bringing this interesting exhibit before the Society, enquired if the interval between the bracts and the new calyx was to be regarded as an elongation of the floral axis?

Dr. HAMSHAW THOMAS commented upon the interest of the specimens, and enquired whether Mr. Worsdell held the view that the petals and sepals of the poppy were to be regarded as sterilized and modified stamens.

Mr. WORSDELL, in reply, said that the displacement of the sepals has been brought about by the development of an internode between the corolla and the calyx. It is almost universally held that the corolla in flowers generally has been derived by transformation of stamens. As regards the question of the stamen being the ancestor and progenitor of all floral members below it, that is too big a question to enter into.

Mammals collected by Lord Cranbrook and Captain F. Kingdon Ward in Upper Burma. By Captain Guy Dollman.

LORD CRANBROOK and Captain Kingdon Ward collected some 300 specimens of Mammalia during their recent expedition to Upper Burma. Many of these represent rare genera, and the collection contains representatives of four new forms. Amongst the latter are a goral from the Adung Valley which it is proposed to name after Lord Cranbrook, as being the most striking novelty in the collection, and a new squirrel, of the genus *Tomeutes*, to be named after Captain Kingdon Ward. The other new forms comprise a bat of the genus *Myotis*, which it is proposed to associate with the name of Lady Cranbrook, and a rat of the genus *Rattus* which would appear to be a very distinct species.

Two monkeys are contained in the collection—a grey langur, which has been determined as *Pithecus shortridgei*, and a pig-tailed macaque, *Macaca nemestrina*. The latter species is represented by a young specimen and a portion of the skin of an adult individual which, together with a piece of skin from a specimen of the new goral, forms part of a native bag brought back from Nam Tamai. Four or five species of bats were obtained, including the new form of *Myotis*, collected, along with most of the other specimens, in the Adung Valley.

The collection is very rich in Insectivora, no less than ten genera being represented, many of which are quite rare. For instance, the series contains specimens of three rare members of the family Talpidae, *Parascaptor leucurus*, an Asiatic mole, and *Scaptonyx fusicaudata affinis* and *Rhynchonax andersoni*, two rare mole-shrews. The specimens of *Scaptonyx*, three in number, were especially welcome, since this genus was only known from a few examples, two of which are in the Natural History Museum. The present specimens have longer tails than the type-specimen of *Scaptonyx fusicaudata affinis*, but the type-locality of *affinis* is not sufficiently far distant to justify the description of another geographical race on this character alone. The specimens of *Rhynchonax andersoni* also form welcome accessions, as this genus was hitherto known only from a series of specimens obtained by Malcolm Anderson during the Duke of Bedford's exploration of Eastern Asia. Both *Scaptonyx* and *Rhynchonax* are, in spite of their appearance, true members of the Talpidae, the skulls being provided with complete zygomatic arches; from their general bodily shape they might easily be mistaken for shrew-mice, just as some of the shrew-moles, such as *Anoursorex* of the family Soricidae, might easily be mistaken for moles. The genus *Rhynchonax*, together with *Scaptonyx*, *Urotrichus*, *Uropsilus*, *Nasillus*, *Dymecodon*, and *Neurotrichus* form a natural group of the Talpidae.

The Soricidae, or true shrews, are represented by six genera, the most outstanding of them being the giant water-shrews *Nectogale* and *Chimarrogale*. There is also a series of the striped shrew, *Sorex bedfordiae*, named by the late Oldfield Thomas after the Duchess of Bedford from a series of specimens sent home by Malcolm Anderson during the Duke of Bedford's exploration of Eastern Asia. The long-tailed shrew, *Soriculus irene*, is represented by a single specimen which has a tail 10 mm. longer than that of the type; other members of this family represented in the collection are *Blarinella wardi*, named after Captain Kingdon Ward by Oldfield Thomas in 1915, *Soriculus caudatus*, *S. sacratus*, and a long series of *Chodsigoa hypsibius*.

The Carnivora are represented by nine genera, including two rare cats, *Profelis temminckii tristis* and *P. t. dominicanorum*. There are also examples of the leopard cat, *Prionailurus bengalensis*, the palm-civet, *Paguma grayi*, and a panda, *Ailurus fulgens*; the last specimen may belong to the eastern form *A. f. styani*.

The collection is particularly rich in rodents, and contains examples of the giant flying squirrel, *Petaurista yunnanensis*, the lesser flying squirrel, *Hylopetes alboniger*, the giant

squirrel, *Ratufa gigantea*, the long-nosed squirrels *Dremomys macmillani* and *D. pernyi*, and the new form of *Tomeutes* referred to above; the latter belongs to the *lokroides* group, and the type was obtained from the Kachin Hills. There is also a large series of the red-bellied squirrel, *Callosciurus erythraeus*, and several dozen rats and voles representing about thirteen species, including the new species of rat, ten specimens of which were collected in the Adung Valley.

The Ungulates collected comprise three species, the Chinese muntjak, a serow, and the new goral. The last is undoubtedly one of the most striking discoveries made in recent years, and Lord Cranbrook and Captain Kingdon Ward are to be congratulated on obtaining this fine new species. Half the collection has been presented by Lord Cranbrook and Captain Kingdon Ward to the British Museum and the other half to the Field Museum of Natural History, Chicago.

LORD CRANBROOK, in giving some account of the collecting trip, referred to the distribution of *Nectogale*, which was seen and caught as low as 5,000 ft., though it had previously only been reported from 12,000 ft. and upwards. The goral, however, did not appear to come down much below 8,000 ft., and in the summer goes up into the open above the tree line (12,000 ft.); the ordinary Himalayan species range downwards to 3,000 or 4,000 ft. According to the natives the goral does not cross the main range, but is probably common on all the hills above 8,000 ft. in this area, as far south as the hills in 'the Triangle' east of Fort Hertz.

Captain KINGDON WARD added some remarks on the geographical distribution of the new goral, stating that it was fairly widely distributed on the Burma and Assam frontiers.

Dr. W. T. CALMAN expressed the indebtedness of the Zoological Department of the British Museum to Lord Cranbrook, Captain Kingdon Ward, and Major Powell-Cotton for the valuable collections which they have presented to the Mammal Section of the Department.

Two skulls of a small race of elephant from the Cameroons and from Sierra Leone. By Captain Guy Dollman.

FROM time to time in recent years many rumours and reports of dwarf elephants have been received, but the evidence at present available tends to show that these dwarf races have been founded on material that is sub-adult or immature. Two subspecies have been described, one from the Congo (*Elephas africanus fransseni*) and one from the Cameroons

(*E. a. pumilio*), but no satisfactory skull material was forthcoming to prove definitely the age of these animals.

The specimens shot by Major P. H. G. Powell-Cotton in the Cameroons, and His Excellency the Governor of Sierra Leone in the Gola Forest definitely prove the existence of a small race or races of elephant existing in West Africa, as both skulls are those of fully adult individuals. In the case of Major Powell-Cotton's specimen the last molar is not only in position, but is well worn along its entire length, and in the case of the Gola Forest specimen this tooth has been in use for some time, as its surface is more than half worn. The ivory in both cases is small, and the general bodily dimensions were also given as being much smaller than those of the large bush elephant. The latter we may call *Elephas africanus capensis* or *oxyotis*, and the small forest elephant may provisionally be known by the name *E. a. cyclotis*.

In a communication from His Excellency the Governor of Sierra Leone it was pointed out that, in addition to the large type of elephant and the small forest elephant, there was existing in the Gola Forest a still smaller animal which was known by the native name of 'Sumbi'. This beast was said to stand only about five feet at the shoulder, and therefore may be reckoned as a really dwarf elephant if the report of its existence proves to be founded on adult material. It is to be hoped that further specimens of West African elephants will be available for examination in the near future to settle this problem of the dwarf elephant once and for all.

MR. H. N. RIDLEY asked Capt. Dollman whether he could give any information as to the reported dwarf elephants of the Siamese marshes, and stated that they were reported to occur near Ton le Sap, and had been seen by a friend of his.

Dr. A. F. G. KERR having spoken, Dr. J. M. DALZIEL asked whether there was any information as to the external appearance of the dwarf elephant of Sierra Leone, the skull of which was exhibited. Local sportsmen in that country had for long been interested in an elephant described as 'white', though the term might mean no more than in the case of the 'white rhinoceros' of another part of Africa. The Governor of Sierra Leone had given three vernacular names for supposed different types of elephant, and the so-called 'white elephant' was no doubt one of them.

Prof. E. W. MACBRIDE said that a question having arisen whether such things as white elephants really existed, he desired to call attention to the fact that a 'white' elephant had been exhibited by the Zoological Society for three or four months. Its skin was pinkish, its hair greyish white, and its eyes pink. It was evidently an albino—i.e. a sport, not a type of a distinct race.

Major P. H. G. POWELL-COTTON said that in the months of February to May the Cameroon dwarf elephant was to be found in small herds of four to eight in the country lying between the Ongue Creek, which connects the rivers N'Yong and Sanaga, and the coast. The forest and undergrowth is very dense, and the ground swampy, with frequent streams and pools that make tracking difficult and arduous. The elephants often visited the plantations during the night, but trekked in the early hours for long distances into the forest. The South Cameroons race frequented the same forest, but usually in somewhat larger herds. On several occasions he had followed the tracks of a small troop of the dwarf elephants (Lokopaka) accompanied by a solitary male of the South Cameroons race (N'Kumbe). According to the natives the latter had been turned out of his troop, and now associated with the Lokopaka for company, but they would not interbreed.

Major Powell-Cotton gave a few measurements :—

Dwarf Race.

	Height.	Circumference, fore foot.	Ear.
Herd ♂	6' 4"	33	39×29
Old adult ♀	6' 8"	37 $\frac{3}{4}$	39×30

South Cameroons Race.

Herd ♂	7' 1"	36 $\frac{1}{2}$	40×31
Old adult ♀	8' 3"	41 $\frac{1}{4}$	43×37 $\frac{1}{2}$

He informed the Society that the complete skins and skeletons may be studied at the Powell-Cotton Museum, Birchington.

Dr. W. T. CALMAN drew attention to the asymmetrical development of the molar teeth of one of the elephant skulls exhibited.

Captain DOLLMAN, in his concluding remarks, referred specially to a specimen of the very rare flightless scaly-tail (*Zenkerella insignis*) received from Mr. Merfield through Major P. H. G. Powell-Cotton. It was collected in the Cameroons, and makes the third specimen of this rare animal received by the Natural History Museum, the other two being a specimen in spirit and a skin and skull received from Mr. G. L. Bates some years ago. The latter specimen formed the basis of the late Mr. de Winton's genus *Aëthura*, which was antedated by a few days by the late Dr. Matschie's description of the specimen received by the Berlin Museum, and named by Dr. Matschie *Zenkerella insignis*.

On *Scolecopteris Oliveri*.—Part II. The vegetative organs.
By D. H. Scott, F.R.S., F.L.S., and H. S. Holden, F.L.S.

THE pinnules of *Scolecopteris Oliveri* are small and fleshy, with rounded apices and reflexed margins. Each is united to the rachis by the whole of its base. The venation is essentially dichotomous in plan. In the proximal two-thirds of the pinnule a midrib is present from which lateral veins are given off, these dichotomizing near their point of departure from the parent strand. Towards the apex of the pinnule the midrib undergoes repeated bifurcation.

The rachis is traversed by a U-shaped bundle, from the margins of which small concave pinnule traces are given off. These traces are endarch and enter the pinnules without branching. All the veins end distally in well-developed hydathodes, characterized by short barrel-shaped tracheids, generally with oval pits.

The upper epidermis of the pinnule consists of regular polygonal cells, and is devoid of dermal appendages. Below the epidermis is a layer of water-storing tissue several cells deep, followed by typical palisade cells and spongy mesophyll. The lower epidermis differs from that of the upper side in possessing stomata and dermal appendages. The stomata occupy the concavities between the ridges underlying the veins. They are very well preserved, and it has been possible to make a detailed study of their structure. The ridges below the veins bear both multicellular hairs andramenta. Associated with the rachises and pinnules are a few crushed axes of larger dimensions, which may possibly be rachises of a higher order. These give off C-shaped strands extra-marginally which are similar in appearance and dimensions to those of the pinnule-bearing rachises.

Comparison with material of *Scolecopteris minor* and *S. elegans* shows that there are well-marked differences between these and *S. Oliveri*.

Dr. D. H. SCOTT congratulated his colleague Prof. Holden on the admirable way in which he had presented the results of their work. The investigation of the vegetative organs had been mainly in Prof. Holden's hands. The detailed account of the stomata in particular was probably the fullest yet given for a fossil plant.

In every respect the anatomical (as well as the reproductive) characters proved to be those of a fern. Great as the difficulties were, he relied on comparative anatomy, and could not doubt that a body of highly organized ferns, with some affinity to existing Marattiaceae, was flourishing in Carboniferous times, side by side with fern-like Spermatophyta.

Dr. HAMSHAW THOMAS said that Prof. Holden's communication was of exceptional interest and importance. We now seemed to have good evidence for the view that the *Scolecopteris* and *Asterotheca* types belonged to true ferns rather than to seed plants. The anatomical details were also of great interest from the standpoint of physiological and ecological anatomy. The structure of the leaves, with their characteristic palisade and subepidermal tissues, suggested a habitat very different from that of the normal Coal Measure plants and much drier. The form, structure, and distribution of the stomata were also of interest to those who had to study the structure of fossil stomata obtained by the maceration of mummified remains. The speaker enquired whether a similar type of structure was known to occur in any recent ferns.

The PRESIDENT, thanking Prof. Holden for the very clear way in which he had explained the anatomy of this interesting specimen, wondered whether the branch bundle described might be connected with stipular growths such as are known to occur in the Marattiaceae.

Professor HOLDEN replied.

10 NOVEMBER 1932

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 27 October 1932, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted:—Wilfred Edward Shewell-Cooper.

Certificates of recommendation of the following candidates for Fellowship were read:—For the second time, in favour of William Charles Osman Hill, Abbas Fathi el-Helaly, John Hugh Davie, Chrystabel Prudence Goldsmith Procter, John Vardy, Reginald Edward Vaughan, and Harold Alexander Wootton; for the first time, in favour of Richard Frederic Nevill Aldrich-Blake.

**A rare marsupial (*Notoryctes typhlops*).
By Captain Guy Dollman.**

A SPECIMEN of the rare marsupial mole (*Notoryctes typhlops*) has recently been presented to the Natural History Museum

by Mrs. Daisy Bates, who for some thirty years has lived in the native camp at Ooldea, South Australia. Mrs. Bates sent home some interesting notes on the habits of this mole-like marsupial, which goes by the name of the 'Arru-jarru-ju' in its own country.

In these notes Mrs. Bates remarks that this mole burrows to a depth of sixty feet, and records having found one of its tunnels twelve feet below the surface. That this species is blind appears to be a well-established fact, but that it is deaf and dumb, as suggested in Mrs. Bates's notes, seems very unlikely. A specimen has been heard to give utterance to a chirping noise, and, although external ears are absent, as they are in so many fossorial mammals, the structure of the skull shows that the internal ear is developed.

On two dugongs from Mafia Island.

By Captain Guy Dollman.

Two skulls of a male and female dugong from Mafia Island, Tanganyika Territory, have recently been presented to the Natural History Museum by Mr. B. W. Savory. On comparing these skulls with specimens from Australia it would seem that the Australian dugong (*Halicore australis*) is a larger and heavier animal than the dugong of East Africa. The two Mafia specimens are shown by their teeth to be old individuals, but they are both much less massive and smaller than examples of similar age from Australian waters.

The tusks in the male dugong, when the animal is adult, are large and well-formed teeth, extending well out beyond the alveolar border. The first pair of incisors are shed early in life, and their alveolar cavities are encroached upon by the rapid and extensive growth of the second incisors or tusks. In the female the tusks are retarded in their growth, much as they are in some female Indian elephants, and never emerge beyond the alveolar border, remaining hidden in the alveolar tissue throughout life.

Another resemblance to the Proboscidae is to be found in the method of succession of the molar teeth, the succession being horizontal, not vertical as in the majority of mammals. The first three cheek-teeth are shed one after another, leaving only the hinder pair in old age. The last tooth, as it wears, becomes more and more bilobed, owing to the grinding away of the upper tuberculate surface, with the result that the lower and centrally constricted region of the tooth comes into play, so that a figure-of-8-like section results. The same holds good for the lower jaw. In the front of this jaw there may be observed four alveolar juts in each ramus, which in early life accommodated the lower

incisors or incisor and canine teeth. These teeth are quite functionless and are, throughout their existence, covered by the horny plate of the lower jaw; they are absorbed at an early age and their alveolar cavities would seem to form some sort of anchorage for the horny plate above them.

Some lantern-slides of one of these Mafia Island dugongs were exhibited, showing to advantage the lateral position of the eyes and ears. The general shape of the animal was compared with that of one of the faked mermaids, so often to be seen in Aden. In these faked individuals one commonly finds the real eyes, ears, and nostrils have been obliterated, and a new and somewhat human-like face built up on the muzzle of the animal. This is sometimes done by skinning the muzzle as thin as possible and allowing the skin to dry over a mask. Sketches of this type of fake were made on the board.

Mr. J. T. CUNNINGHAM asked if the pectoral position of the mammary glands was not another character in which the dugong and manatee resembled the elephant.

Professor E. W. MACBRIDE referred to reports of a dugong occurring in S.W. Africa; it appeared, from the evidence at present available, more likely to be a manatee.

The old morphology and the new.

By Dr. H. Hamshaw Thomas.

The study of Comparative Morphology has attracted so little interest in recent years in England that it is almost necessary to apologize for bringing forward to-day some general morphological considerations. Many of those who were formerly workers in the subject have felt that it was not leading to anything of importance, others have regarded morphology as merely concerned with the description of fact. There is even a fundamental disagreement as to what constitutes morphology, and some of our German colleagues would like to exclude the greater part of the matter which usually appears in text-books under this heading (Troll, W., 1928, p. 61) and retain only the comparative study of external form. They consider, too, that phylogenetic questions should be rigorously excluded, though they themselves clearly find this very difficult. I believe, however, that most English botanists would agree with Prof. Bower's concise statement that 'the full problem of morphology is . . . to explain . . . how in the past plants came to be such as we now see them' (1908, p. 7). The explanation is not only of intrinsic interest, but it is also required to afford a sound basis for taxonomic work.

If we survey the whole field of recent morphological

investigation we find the significant fact that a great and increasing gulf has arisen between the concepts of angiosperm and pteridophyte morphology. In dealing with the angiosperms most modern writers accept the doctrines of the classical system, a system which originated in days before the coming of evolution, when the constancy of species was an axiom. The morphological nature and relations of the higher plants as generally envisaged are still almost exactly the same as conceived by Goethe, Lindley, and de Candolle a century or more ago. They are conclusions based on ideas in which evolution had no place, and they are supported by arguments (Velenovsky, 1905; Troll, 1928) which are precisely the same as Goethe used in 1790. In contrast to this we find that during the last twenty years a large body of facts has been accumulating about the simpler and older plants. We now know a good deal about the details of structure of the Pteridophyta, ancient and modern, much about the Gymnosperms, while the works of Kidston, Lang, and of Kräusel and Weyland have given us a general idea of several of the plant types of the Lower and Middle Devonian period. We know what actually constitutes a primitive land-plant form, and have a general scheme in which the evidence from comparative study agrees with that from the fossils. I do not think that as yet any statement has been made as to the bearing of this new knowledge on the classical theory, but I know that many botanists who are familiar with the facts are sensible of a considerable modification of their views, and are adopting, at least for the Pteridophyta, a system of morphological concepts which are quite at variance with the old classical concepts. At the same time the old formal and idealistic morphology still exerts a strong influence on botanical thought, especially on the continent.

The questions before us are 'How do the doctrines of the new morphology affect those of the old', and 'Do the recent discoveries in the field of the Pteridophyta and palaeobotany bring anything of value to the student of the higher plants'? I do not expect to be able to give complete answers to these questions, but I hope to put forward some considerations which may be of general interest and to ask those who are concerned with systematic botany to consider them. I have been compelled to give considerable thought to the subject, for I have been trying for the last twenty years to bridge the gap between Gymnosperms and Angiosperms by studies on the floras of the Mesozoic period, and some of the newly discovered forms require at least a provisional solution of the problem.

At the outset of any discussion on the study of form it is necessary to keep in mind the principles underlying a

comparison of plants or their parts. We may, and habitually do, compare forms along two distinct lines of reasoning, which we may term the subjective and the objective, and which correspond, at least in part, to the old philosophical distinction between the idea and the thing. The subjective approach is purely a psychological process, for while to a certain extent any comparison is a mental operation, many of our comparisons are solely the result of impressions gained by the senses and have no absolute validity. By this I mean that the objects compared have no genetic connection, but are only comparable owing to some property or attribute. Thus we habitually institute a comparison—by using the name globe—between the earth, a wooden sphere covered with the map of the world, a hollow sphere of glass, and in certain athletic circles a leather-covered india-rubber ball. The only connection between these objects is that they are approximately spherical in shape. It has been argued (Troll, 1928, p. 5) that morphology, dealing only with form, should depend only on our sense of sight, and has no concern with the materials out of which forms are built; but if this is so, the subject is scarcely worthy of further consideration.

Most scientists, however, aim at an objective approach to their objects of study. In modern morphology we attempt to compare structures with a view to determining their genetical relationships. We can compare objectively the earth and the moon, the seedling and the adult tree, the different individuals composing the offspring of a single plant. Here the connection of the objects does not depend on the sense of the observer.

Of course the boundary between the objective and the subjective is very ill defined. When we try to imagine a primitive form connecting two known plants we relapse into subjectivity, and can only escape from it by discovering some fossil which is like the form which we have imagined. It may well be that many of our suggested connecting links have only existed in the imagination. Hence in trying to prove relationship it is important to obtain evidence from a number of unconnected sources, so that our conclusions, though incapable of objective demonstration, have a high degree of probability. This is one of the reasons why the morphology which deals only with external form can carry little weight.

The morphology of the early observers, with the possible exception of some of the rather curious ideas of Linnaeus, was purely subjective. It is absurd to say that because the study of form originated in this way it must for ever remain so; the history of the study is of a gradual advance from the subjective to the objective attitude, and of the

attempts to realize the significance of structure in the life of the plant rather than in the eyes of man.

The foundation of the classical system of morphology, and the introduction of the term morphology, were due to the poet philosopher Goethe. His approach to the subject was essentially humanistic, but was that of a well-trained thinker. For some years he had devoted himself to writing and to philosophical speculation, and probably under the influence of Kant he turned towards the world of Nature. In the world of plants and animals Goethe became aware of immense variety of forms, differing greatly in their outward appearance; his task was to discover some principle of unity throughout, and his most important conclusions were published in 1790 in a treatise on the Metamorphosis of Plants. This has been called 'the foundation of all that has been subsequently done in vegetable morphology' (Seeman, ed. note to translation of Goethe's Metamorphosis, Journ. Bot. 1863). The most important conclusion in this essay is that 'whether a plant produces leaf buds, flowers or fruit, it is still the self-same organ which is carrying nature's laws into effect, though performing different offices and disguised under different forms. The same organ which on the stem expands as the leaf exhibiting every variety of form is contracted in the calyx, again expands in the petal, is once more contracted in the stamen and pistils, to expand for the last time in the fruit'. This one organ is called the leaf, but Goethe appeared to feel that it should be given some more general designation. Thus the philosopher perceived unity in variety: he later attempted a similar task in the animal kingdom, finding his unifying structures in the vertebrae. It is striking that the important place which Goethe occupies in the development of botanical thought rests almost entirely on this early essay, which in many respects is an example of clear logical thought; the later development of his nature-philosophy shows how far his mind could range into the mists of speculation.

The foundation of Goethe's doctrine is that when we look at plants we may observe three types of change or metamorphosis—regular, irregular, and accidental. To quote again from the English translation: 'Regular metamorphosis may be observed constantly and gradually at work from the first seed-leaves to the mature fruit, mounting upwards as by an imaginary ladder to that crowning aim of Nature, the production of male and female organs'. Irregular metamorphosis is the case where Nature takes one or more steps backwards, and instances are provided by abnormal flowers. Accidental metamorphosis is that produced by external causes, especially through the operation of insects, but they

were not considered, as they might lead one away from the plain path.

Sachs, in his 'History of Botany', considered that Goethe never made any distinction between the figurative expression metamorphosis and an actual change such as may be said to occur in abnormal flowers: the word is sometimes used in the literal and sometimes in the figurative sense. But while the doctrine of the constancy of species held sway it was scarcely possible to regard metamorphosis as having anything but a subjective significance, and in a later work Goethe stated his idealistic outlook more clearly.

It is necessary to pay particular attention to this work, because it embodies the most important doctrine in the classical morphology, an idea which has been regarded as axiomatic since the early days of the nineteenth century. For a time the term morphology referred only to the study of the changes which can be observed in the form of the leaves. Its spread in England must have been largely due to the part played by Lindley (1832), who devoted to it several chapters of his 'Introduction to Botany'. In this work we find the repetition of Goethe's views and Goethe's arguments, viz. that there is a continued uninterrupted passage from leaves to bracts, from bracts to the calyx, and so on to the pistil, also that there is a tendency on the part of every one of the parts to revert to the form of the leaf. There is one important difference between Lindley's views and those of Goethe which has not hitherto received attention. Goethe says near the close of his essay: 'The thing now to be aimed at is to keep habitually in view the two contrary directions in which variations are developed. For we may say with equal truth that a stamen is a diminished petal or that a petal is an expanded stamen' (trans. Cox, 1863, p. 373). Lindley (1832, p. 79), on the other hand, remarks: 'The leaf, as the first formed, the most perfect of all (the appendages), and that which is most constantly present, is properly considered the type from which all the others are derivations'. This is an assumption for which no further argument or evidence is brought forward, but it became an integral part of the doctrine. Lindley states that in 1832 Goethe's theory is universally accepted by all philosophical botanists, and some twenty-seven years later Darwin, in the 'Origin of Species', spoke of the view that the parts of the flower consist of metamorphosed leaves as familiar to almost everyone.

And from Darwin's time to the present day the old concepts of the subjective and idealistic philosophers were taken over by the evolutionists and given an objective significance. The researches of Hofmeister provided a basis for the

formulation of a general scheme, but unfortunately botanists, while drawing perfectly valid comparisons, continued to use the old nomenclature to express these comparisons.

Although the idea of metamorphosis forms the basis of the classical morphology, the principle of the categories is closely connected with it. In the earlier writings the axis and root seem to be treated as the fundamental parts of the plant on which the various appendages are carried. Later a sharp distinction was drawn between leaves, shoots, and roots, and all were included in the scope of morphology. However, this doctrine of categories has not met with universal approbation, and we have had the phytonic hypothesis, the pericaulome theory, and the leaf skin theory of the stem.

The recognition of three categories of organs, and three only, may have been possible when we had to deal only with the most highly evolved plants, but it was bound to lead to difficulties when an attempt was made to extend it downwards. It has resulted in an unnatural separation of the Thallophyta and Bryophyta from the higher forms. If only the early evolutionists had started afresh, and instituted a terminology based on the structure seen in the lower plants, the present impasse between the new morphology and the old would not have arisen.

I think that it can be stated without hesitation that the major points in the classical theory have come in the course of time to be considered so axiomatic that nobody has bothered about the evidence on which they were based, and few have endeavoured to follow up its implications. After 140 years of metamorphosis and comparative morphology we have learned little or nothing about the probable origin of the flower. A Norwegian botanical colleague remarked to me recently that most botanists on the continent of Europe have been taught that stamens, carpels, and petals are modified leaves, and left with the impression that the earliest plants possessed foliage leaves without any reproductive structures. There can be no doubt that a most important advance was made in morphology when Prof. Bower (1908, p. 702) put forward the view that all parts of the plant could be regarded as potentially sporogenous, so that branches may bear sporangia as well as leaves. Although Goethe had asserted that we could say that the petals were expanded stamens, few authors have translated this into an objective statement and followed up its implications, though it rests on just the same evidence from comparative study as the contrary view. When authors, like Prof. Troll (1932, p. 298), speak of comparative morphology as the only safe method of investigation they forget that comparative method seldom, if ever, shows which end of a series of forms is the more primitive.

As a matter of fact we cannot feel sure to-day that the lateral aerial organs of the flowering plant are homologous structures or that the stamens and carpels are not more comparable with modified branches than with foliage leaves. The true classical morphologists rule out all arguments other than those based on a comparison of the development and of the mature forms of organs, and those based on abnormal forms. Such arguments would have some force if they could be completely substantiated and if a developing carpel could be turned into a foliage leaf in the same way as the rhizophores of *Selaginella* can often be turned into leafy stems. Recently, however, Prof. Victoire Grégoire (1931) has entered the field with the declaration that the stamens and carpels are organs *sui generis*, because from the first their primordia can be distinguished from those of foliage leaves and are not identical with leaf primordia as generally supposed. The fact that in abnormal flowers a leaf-like structure springs from the place in which one would expect a carpel or a stamen does not prove that the latter is a modified leaf, for a stem may continue to grow without producing carpels or stamens at all.

The validity of many of the arguments from abnormal flowers was challenged some years ago by Goebel, and more recently by Mrs. Arber (1919, p. 70), who rightly pointed out that while much evidence has been brought forward in support of the principle of irreversibility in evolution, little or nothing can be urged against it apart from the case of meristic variations. Meristic variations, however, have little value in this connection, and, as recently shown by Prof. Schoute (1932, p. 164), are better explained in another way. Mrs. Arber's application of Dollo's Law to plants seems to have received comparatively little attention, and it is therefore worth while to note that an authoritative statement has recently been made from the standpoint of the palaeozoologist by Dr. Bather (1928, p. 87), who, in addressing the Geological Society, said 'Dollo's Law is a simple statement of fact based on the evidence of fossils'.

In view of these considerations we may say that the two main arguments of the classical morphologist cannot be regarded as in any way conclusive, and may well turn out to be worthless. We are then left solely with the argument of progressive differentiation during development, a consideration which has no final significance, and can, as Goethe noticed, be used in the reverse sense.

Now, as is well known, the rise of the doctrine of evolution led to a great outburst of morphological activity among botanists, and a search for new criteria of primitive types. It might well be expected that at least some of the work

done on comparative anatomy, on development, or on the study of fossil plants might be useful in connection with angiosperm morphology; but although many English morphologists are prepared to take these studies into account, the real champions of the old ideas will not do so. Velenovsky (1905, p. 7), in one of the last general surveys of Comparative Morphology (published 1905-13), rejected both the study of ontogeny and anatomy as useless, while during the last few weeks I have been accused by Prof. Troll (1932, p. 298) of falling into the old error of thinking that the vascular structure of the carpel could have any morphological significance. In reply, one can only say that in groups like the Ferns, Lycopods, and certain Gymnosperms, where we possess a good deal of definite phylogenetic information, both ontogenic studies and vascular anatomy have been shown to have very considerable significance, and there is every reason to suppose that the same is the case in the Angiosperms. I am tempted to conclude, from Prof. Troll's recent paper, that the evidence from vascular structure is regarded as valid if it supports the orthodox arguments, but not otherwise. I sometimes suspect that the real reason for rejecting the evidence of vascular studies and of ontogeny is that they are known to give no support to the classical concepts, and are therefore put on one side as useless.

As I see it to-day the classical system of morphology, with all its implications for taxonomy, is a great edifice built on sand which crumbles away whenever it is closely investigated. This edifice has stood until now, not because it was well built, but because of the stability which successive generations have attributed to it. It is only when we cease to revere it that we recognize what a flimsy structure it is.

One may criticise the classical morphology, but is there any more satisfactory system to put in its place? There is certainly nothing so concise or dogmatic which can be applied with equal force to all vascular plants, but a series of general ideas are emerging which may later prove to have universal significance. In endeavouring to build up a new system of morphological ideas we must take into consideration the evidence derived from the study of all aspects of plant-life. The old clear-cut distinction between plant physiology and plant morphology is a legacy of subjective thought. There can be no sharp distinction between form and function, for form depends on the physical properties of the organism and the mechanics of cell construction. We know, too, that form is related to cytological considerations, while the results of genetical work must be kept in mind. If we wish to understand the variations in the shape of plants, ancient and modern, it is necessary to consider the relation of form

to the conditions of the environment, and this requires a recognition of the ideas put forward by workers on terrestrial physics and palaeoclimatology.

The general ideas of the new morphology, if one may use this term to cover ideas some of which found expression twenty-four years ago in Lignier's 'Essay on Morphological Evolution' (1908), Bower's 'Origin of a Land Flora' (1908), and Tansley's 'Filicinean Vascular System' (1908, p. 9), are based on considerations of phylogeny. If all green plants have sprung from a common stock, like the branches and twigs of a tree, then the relations between the various forms can be explained only by reference to the branches from which they have sprung. Phylogenetic morphology has been held up to scorn by some writers, while others have considered it to be a hopeless quest. I believe it has appeared hopeless because a continual attempt has been made to graft new facts on to an old system which has little or no actual basis of truth. It has been more than once stated that the discoveries of fossil plants have raised more problems than they have solved, but probably many of the problems thus raised may appear much less formidable if we can get rid of the bias engendered by the classical traditions. Reverting to the metaphor of the tree, it is clearly impossible to try to reconstruct all the branches, but here and there we may get glimpses of some of the lower branches which give us an idea of what has been going on in the past. The idea of parallel evolution is an important one. If we can ascertain what has gone on in the Ferns it may help us to understand the evolution of the Gymnosperms, for there is good reason to suppose that all the higher plants have a fundamentally similar physical and chemical constitution. The classes Pteridophyta, Gymnosperms, and Angiosperms may, indeed, represent stages in evolution rather than independent groups springing from common ancestors.

No doubt specialization is to be found everywhere in varying degrees, and we must try to recognize the difference between specialization and more general evolutionary tendencies. I believe that the geological record may well prove to be more complete than we have previously believed, though without doubt many forms remain to be discovered. Although most of our fossil floras represent the remains of marsh-plants, it is probable that they contain samples of the chief types of contemporary plants. Probably few of these plants are the direct ancestors of modern forms; it is more likely that many represent lines near the lower branches, which became cut off through over specialization, and were unfit to survive under alterations of climatic conditions which periodically occurred. But these relics may

furnish clues as to the stage of evolution of their more successful competitors of the same period. It must be remembered, too, that many of our fossil floras are as yet imperfectly investigated, and that while many leaves are known, the reproductive structures are only slowly being brought to light. Thus some of the leaves, such as *Sagenopteris* and *Thinnfeldia*, which have been figured in the older books as ferns, were almost certainly the leaves of seed-plants.

It seems to me that any system of morphological ideas must be applicable to all land-plants. There is only one group in which the comparative morphology has been worked out on the new phyletic lines. Prof. Bower's work on the Ferns (1923-1928) has provided us with evidence drawn from a number of different aspects as to the probable evolution of this group. I believe that the same principles which apply to the Ferns apply also to other groups. Zimmermann (1930) has attempted a comprehensive work from this standpoint, and his treatment of the Gymnosperms is most interesting.

If we may select a few of the more important points which seem to emerge from the study of the Pteridophyta and of the earlier fossil plants we may notice:—

(1) The more primitive land-plants were probably of the *Rhynia* or *Asteroxylon* type, in which the main differentiation was into fertile and sterile parts. Recent work on the Devonian floras shows that these plants were in important respects typical of the contemporary stage of evolution rather than specialized types. They link on to the sporophytes of the Bryophyta on the one hand and to the Lower Carboniferous frond-forms on the other. There was originally little or no morphological distinction between roots, stems, and leaves.

(2) In most cases there is an early differentiation between stems and roots, and also between the simple microphylls and the branch systems or 'telomes' which later evolved into the megaphylls of the higher plants. Leaves may probably be divided into two categories quite as distinct as those of roots and stems.

(3) Megaphylls were at first specialized lateral branch systems, and for a long time continued to be more like branches than leaves. The common *Sphenopteris* forms of the Upper Devonian and Lower Carboniferous illustrate this type. These flattened side branches tend to become aggregated in fan-shaped groups which develop lateral webbing; so we get to the large repeatedly branched fronds of the Upper Carboniferous with lateral pinnules having an open venation. Later the fronds became reduced in size and the pinnule nervation shows anastomosis.

(4) The fertile branches long remained as relatively narrow terminal structures either as separate branch systems or associated with foliage development. I think that it is only by reference to this origin that we can regard the stamens and carpels of the Angiosperms as homologous with leaves; they are equally homologous with branches.

(5) The simple type of leaf with its anastomosing veins would thus be regarded as the most highly evolved type rather than a primitive form.

(6) In the more primitive types the terminal sporangia were borne either singly or in groups. As foliar development proceeded the sporangia may have either retained their original position on naked branches or have become involved in frond formation, and in this case attain either a marginal or a superficial position as in most modern ferns. Groups of sporangia may have become more or less united, and potentially sporogenous tissue may have become sterilized.

(7) As regards vascular anatomy, we first find a distinction between stem and root, and between main stem and lateral branch systems. The original small stele expanded and became medullated, the centripetal wood disappeared from the stem, remaining in the root. Rows of tracheids finally became vessels in the highest forms.

It is obvious that these generalizations are quite inconsistent with the scheme of the classical morphology: they seriously restrict the idea of the three distinct categories of organs, and modify our views of homologous structures. The idea of categories may still be useful in dealing with a single advanced group, but I think that the reproductive structures in all plants should no longer be placed in the category of leaves, since this term implies foliar specialization.

I believe that if morphology is to advance we must examine the definition of all our morphological terms in the light of phylogeny, and we shall probably require a number of new terms. For example, the term sporophyll is universally used for a sporangium-bearing structure, but if the divided leaf is a specialized branch system it is doubtful whether the antherophore of *Ephedra* or the anther of a flowering plant have ever reached the stage when they could be called leaves. What we need is a terminology which expresses the relations of parts to each other, not only as we see them to-day but also in time. The phyletic method of objective comparison requires a standard of values quite different from that of the classical system.

Now you may well ask if this 'so-called' new morphology can give us any help in understanding the seed-plants? I believe that it can. Take first the Gymnosperms. Here many difficulties were encountered in fitting the reproductive

structures into the classical scheme. The case of the ovuliferous scale in the Coniferae is well known, while the classical interpretation of the female inflorescence of several members of the Gnetales required the postulation of former seed-bearing leaves which had disappeared without leaving the faintest trace of their presence. The new morphology provides a simple and uniform system by which almost all the fertile structures can be explained. The sporangia were originally terminal, and while this position is generally retained frond formation has progressed in varying degrees in certain forms.

In *Ginkgo*, the Bennettitales, the Cordaitales, and the Gnetales the ovules are terminal structures, while the same is probably true of the ovules of the Taxoideae. The ovuliferous scale of the Abietineae now shows little signs of being a flattened and united branch system bearing ovules near its base, but the Permian *Voltzia* showed some indications of such an origin. The Cycads have always been the mainstay of the idea that ovules were originally produced as marginal structures on foliar organs. They can equally well be explained on the view that the ovuliferous structure of *Cycas* is a lateral branch system or telome in which the lower branches bear terminal ovules while the upper branches are sterile and are webbed. In *Dioon* the number of ovules is reduced to two while the union of the upper portion is more complete, and forms like *Zamia* or *Encephalartos* have almost lost the upper sterile portion. The Pteridospermae will be dealt with later. The microsporangium-bearing structures are capable of the same type of explanation, but it must be noted that the concepts of the new morphology tend to accentuate the separation of the Conifers from the megaphyllous gymnosperms.

We now come to the question of whether these newer ideas are in any way applicable to the flowering plants. Can the essential parts of the flower be derived from structures which are morphologically comparable to those of the Gymnosperms? In this field our current ideas of the morphology of the flower are so closely connected with the classical concepts that there seems at first sight to be no support for the newer views. But one wonders what would result if we started to examine the flowering plants afresh from the standpoint of the new concepts. Might it not lead to a more intelligible view of floral evolution?

It is a far cry from the Psilophytales to the flowering plants, but I believe they may be connected through the Lower and Upper Carboniferous Pteridospermae. A number of arguments can be brought forward for considering that the flowering plants may have been derived from plants

of pteridospermous nature, and it must be remembered that the Angiospermae and Pteridospermae may represent forms in different stages of evolution rather than independent groups derived from a single common ancestor: I have already suggested the derivation of the carpels of the *Caltha* type from the pteridosperms *viâ* a structure of the *Caytonia* type (Thomas, H. H. 1931, p. 656). We now know of structures (Corystospermaceae) from the Triassic which link the Caytoniales closer to the Palaeozoic pteridosperms. They possess some interesting morphological features, for the seed-bearing structures, which by comparison with the pteridosperms would be called sporophylls, must by reference to modern plants be called inflorescences. They are narrow branching structures quite distinct from the foliage leaves, and bear small bracts subtending lateral branches, each of which bore two or three stalked cupulate ovules, with, in some species, a pair of bracteoles. The cupules are recurved, pendulous, and almost entire; they surrounded the young ovule completely, but were open at the base, and the micropyles projected through the opening.

If we examine the forms of leaves from the phyletic standpoint it seems impossible to avoid the conclusion that compound types must be regarded as more primitive than simple ones, and probably that simple leaves with stipules represent a stage in evolution from the compound types. The stipules may perhaps be compared with the peculiar basal pinnae or aphlebiae of the pteridosperms. Of course, leaves of the *Phoenix* type cannot here be regarded as primitively compound, although the Palms are a comparatively old group. The questions of leaf form, petiolar structure, and stomatal structure should be reinvestigated, to ascertain whether or not any similarities with the Pteridospermae can be found. A leaf like that of *Lyonothamnus floribundus*, the Santa Catalina endemic, is especially interesting, since it can be matched very closely with forms from the Upper Trias. Its stomata and its venation come very near to some of the Triassic types. Leaf forms in which there is an equal dichotomy of the mid-rib or mid-vein might prove interesting, and also those which are decompound. Those who have investigated the anatomical structure of the Angiosperms have seldom attempted to institute comparison with the Pteridosperms; but such features as medullary bundles suggest that points of contact may be found.

Turning again to floral structures, there are some points in connection with stamens which I should like to notice. If we go right back to the Devonian period we find plants with well-developed stems, secondary thickening, and large fronds or branch systems with narrow segments; probably

heterosporous had already appeared, but the microsporangia are produced in tufts at the ends of fertile branches. In the Lower Carboniferous there are genera like *Calathiops* in which the sporangia are becoming aggregated by the reduction of the branches on which they were borne, and these lead through *Telangium affine* to *Telangium bifidum*, where the sporangia or synangia appear to arise from the disc-like termination of a fertile branch. Then in the Upper Carboniferous the sporangiferous disc becomes much more pronounced in *Crossotheca*, while in the *Potoniea* type we have a cup-like structure lined with synangia, and in *Whittleseya* and *Aulacotheca*, investigated by Halle, the sporangia are fused inside a more or less solid cylindrical structure. In the Upper Carboniferous and Permian we also find the fertile branches becoming involved in lamina formation, to give structures like *Dactylotheca*, and, if they are pteridospermous, species of *Asterotheca*. It is doubtful whether these later lines of evolution, however, have lead towards the Angiosperms, for in the Triassic form which I have named *Pteruchus* we find the *Crossotheca* type persisting and giving rise to further variations. In the Upper Triassic and Jurassic we find branched structures with bunches of sporangia, very like anthers in the Caytoniales, free in *Lepidopteris*, but united into large bean-shaped synangia in *Hydropterangium* and most Bennettitales. If it is possible to conceive of the reduction of the *Antholithus Arberi* type of the Caytoniales to a single stalked anther, we arrive at the *Ranunculus* type of stamen; but if we imagine the reduction of the *Pteruchus* structure to a single disc, we arrive at a structure very comparable to the male flower of *Populus* or *Juglans*. That reduction of the sterile parts has taken place in the evolution of many modern flowers is a commonplace, and so we have a scheme for the evolution of stamens from the earliest known type of microsporangia-bearing structures along the lines of new morphological concepts. This scheme involves the idea, which may be of some interest, that the male flower of *Populus* may not be strictly comparable with the flower of *Ranunculus*. It also suggests that the possession of branched stamens may be a primitive character. The explanation of such structures as are seen in *Ricinus*, some of the Hypericums, and other plants has always been a difficulty; the hypothesis of *dédoublement*, most usually relied upon, has recently been severely criticized by Schoute (1932, p. 168), and has never rested on any firm foundation. Can it be only a coincidence that *Aptiana*, one of the oldest known types of angiospermous wood, has been identified as a member of the Ternstroemiaceae, a family in which the *dédoublement* hypothesis has been applied to explain the stamens, which show distinct signs of branching?

The usual interpretation of the flower as corresponding to a bud composed of an axis with lateral members seems to be unassailable in the case of certain flowers, but I trust that my suggestion of another origin of certain simple unisexual flowers is not unreasonable. The consideration of the fossils mentioned above leads, however, to the recognition of a further possibility. We can regard the male flowers of the poplar and the sporangiophores of *Pteruchus* as descended from a tassel-like group of equivalent fertile branches, each terminating in a microsporangium; it is conceivable that megasporangia might have been borne in a somewhat similar way. In the female strobili of the Bennettitales all the members seem to be of exactly the same age, and I have seen no specimens in which there are signs of a gradual development from the base upwards such as is seen in a *Caltha* flower. This suggests some such derivation as I have indicated. Other structures which seem to require this derivation are the seed-bearing heads of the Pteridosperm *Lepidopteris*, discovered almost simultaneously by Dr. Harris from Greenland and by myself in South Africa. Is it out of the question to imagine a similar origin for the carpels of some of our flowering plants?

Such speculations in themselves may be valueless except in so far as they suggest ways in which floral evolution may have come about other than those generally recognized. If floral evolution has been going on since the Carboniferous period it is not surprising that we have such widely divergent forms living to-day. I myself feel convinced that the flowering plants must have their origin in the very far distant past, probably in Permian or Lower Triassic times, when, owing to the almost world-wide prevalence of arid conditions, few plants were preserved. There is still hope that in some remote corner of the world we may find fossil flowers which will help to clear up the problem. Two poorly preserved specimens, representing new types of unknown affinities, recently found in the Middle Triassic beds of a remote spot in South Africa, bear some resemblance to flowers and remind us that there is much palaeobotanical work to be done; but in the meantime it may be interesting for those who have the chance of studying living Angiosperms to know what is the trend of the new morphological thought.

In bringing this subject to your notice I do not wish to be regarded as one who delights in wild speculations, or who enjoys an outburst of iconoclasm; but one of the commonest methods employed by researchers in the physical sciences and in physiology consists in observing facts and arranging them in a series expressed by a curve. To ascertain what the observations imply a number of successive assumptions are made, translated into curves by means of formulae,

and the resulting curves are compared with those derived from the initial observations. A good fit is regarded as evidence that a particular set of assumptions provide a possible explanation of the observed facts. Can we not follow a comparable procedure in morphology? The Old Morphology provided only *one* set of assumptions, and we have endeavoured to fit our facts on to them, discarding or distorting those which seemed inconsistent. I have above suggested a different set of assumptions which seem to fit the facts closely, but I am quite prepared to find that on scrutiny serious discrepancies will be revealed. If this is so, we must try once more, altering, as it were, some of the terms in our equation. I am convinced that if Comparative Morphology is to rank with Physiology, Cytology, and other branches of modern Botany, it can only come through a recognition of at least some of the considerations which I have attempted to put forward.

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The BOTANICAL SECRETARY read the following communication from Professor F. O. Bower :—

In welcoming this paper by Dr. Hamshaw Thomas I may be permitted to give a brief historical sketch, which may help to relate the present discussion with what has gone before. The theoretical basis of my own investigations on Archegoniate plants towards the end of the last century was, at the time when they began, almost revolutionary—viz., to proceed by induction from the simpler types of organization rather than by deduction from ideas drawn from types higher in the scale. It was felt that the argument must be evolutionary rather than that of the pre-Darwinian idealists, of whom Goethe was the greatest. This general principle led to a proper evaluation of the phases of the life-cycle. The relative constancy of an alternating succession of gametophyte and sporophyte in land-living plants seemed decisive, for them at least, in favour of a theory of antithetic alternation. This conclusion I still hold, together with the probability of progressive sterilization having been an essential feature of advance. Along these lines the origin of the unbranched sporogonium of the Bryophytes seemed readily intelligible.

The step to a sporophyte of more complicated form was then the morphological Rubicon. In 1894 I propounded a theory of the strobilus as accounting for the origin of the polysporangiate state seen in vascular plants. Two alternatives presented themselves, viz. septation and branching. I relied chiefly on septation, and that wrecked my theory of the strobilus for the time being. The more extended area of fact now available indicates ramification as the chief source of the polysporangiate state, as it is also of the cladode megaphyll. But in the paper read to the British Association at Oxford in 1894 there was a definite suggestion of 'enation' of new parts from a surface previously smooth as a source of new appendages. This idea comes now prominently forward in the origination of 'microphylls' as distinct from the cladode megaphylls resulting from distal branching. In its essentials much of the old theory of the strobilus may yet stand; but it requires to be recast in view of increasing positive knowledge of ramification in early vascular plants. We may start from a Bryophyte type with a distal capsule, which accords with Zimmermann's conception of the 'telome'. Branching of the telome, with dichopodial development, would give a step towards the cladode megaphyll, with all its terminals potentially fertile though not always so developed. Such a state is now before us in the restorations of the Rhynie plants by Kidston and Lang. This, followed by dichopodial differentiation of axis and leaf, which I had already suggested

in 1884 (Phil. Trans. part ii, p. 605), gives a possible source for the simplest type of fern-shoot, based on distal branching only, and with cladode megaphylls bearing distal or marginal sporangia as the result.

But we have now in *Asteroxylon* a suggestion of added microphylls, or, as they might be called, Thursophytoid leaves. These are comparable in position though not in structure with the dermal appendages of Ferns. There is a growing body of evidence that microphylls were of the nature of enations, not of distal branchings as are also the dermal scales of Ferns. Lang's recent work on *Psilophyton* (Phil. Trans. B, vol. cccix, p. 421) suggests that such appendages originated as relatively simple structures, but that they illustrate successive steps towards a more ample development. Something similar is seen in the so-called leaves of the living *Psilotales*. In all of these plants there is a basal region without such appendages. Conversely, in *Asteroxylon* they are not associated with the distal sporangia; the fertile branches appear to bear sporangia only. The same is seen in the distal fertile region of *Zosterophyllum*, a plant without any microphylls, as has been lately demonstrated by Lang (Phil. Trans. B, vol. cccix, p. 133). In fact the fertile cladode or megaphyll and the sterile enation or microphyll may exist quite separately, though they may both be present on the same individual plant. But suppose that microphylls invade a condensed fertile region of telomes, and associate themselves with individual sporangia or sporangiophores, forming thus a compound group of organs themselves referable to more than one distinct evolutionary origin: we should have then a strobilus of the type seen in certain microphyllous Pteridophytes. That this was the composite nature of the Equisetoid strobilus with its well-known fluctuations was fully argued in 1908, in Chapter XXVII of the 'Land Flora'. That view has since been developed by various writers, with the aid of facts more recently acquired. It may also be applied to the Sphenophylls, and now, through Lang's demonstration of the details in *Zosterophyllum*, it appears that it will be equally applicable to the Lycopod strobilus. In all of these we may see suggestions of the building-up of a compound distal cone.

There for the moment we may leave the Pteridophytes, and take up the question of applying a similar analysis to the strobili or flowers of primitive seed-plants, which is the subject of this evening's discussion. I am grateful for having been permitted to see the text of Dr. Hamshaw Thomas's paper. Therein he proposes to carry forward ideas, similar to those briefly sketched above, into the study of early Mesozoic types, and ultimately applying them to those seed-plants of the present day which are commonly held to be relatively primitive.

This application will present difficulties which he will be specially fitted to meet. The first step he is now taking when he states his working hypothesis; but the further removed from a primitive state the objects to which the hypothesis is applied, the greater the difficulties are likely to appear. One special source of perplexity, which is already present in the simpler Pteridophytes, is this: that though the actual initiation of fertile cladodes and sterile microphylls may have been in the first instance distinct, in their later evolution—and particularly where they are specialized for like functions such as photosynthesis or protection—the two types will tend to become indistinguishable. It may even be found that occasional sporangia may be borne upon parts not normally fertile by descent. On this reference may be made to works on teratology. Another point of difficulty will be to accept or reject questions of polyphyletic origin of either or both. But such difficulties will have to be faced by anyone who enters on such a line of enquiry as this. Personally I believe now, as I have always tacitly held, that some such hypothesis as this of Dr. Thomas is the correct way to approach the complex question of floral morphology. The flower of a seed-plant should be held to be a strobilus, just as much as the cone of a Pteridophyte; and from our experience of the latter we should be prepared to regard it as a compound group of organs, composed not necessarily of parts of only one category as regards evolutionary origin. If the composite nature of the strobilus in Pteridophytes be admitted, it cannot rightly be assumed that a flower is the product of an axis bearing appendages only of one type, some with and some without sporangia. A fresh analysis of floral construction is therefore demanded; but in carrying it out one fundamental feature must be borne in mind, viz., that from an evolutionary point of view spore-bearing organs of some sort have been constantly present throughout descent. Normally produced sporangia antedated any other constituent part of the flower upon which those sporangia are now borne.

The BOTANICAL SECRETARY then read the following extracts from a letter he had received from Dr. A. B. Rendle :—

‘The following point of view, arguing from the flowering plant, should not be overlooked. There seems strong evidence that foliage and floral leaves belong to the same morphological category. They are comparable in their manner of development from the axis.

‘The frequent conversion of floral leaves into structures indistinguishable from foliage leaves—they may even bear axillary buds—argues for a common morphological value.

‘One cannot draw the line between sporophylls and the

members of the floral envelope. Carpels and stamens may become petaloid, petals and sepals may be indistinguishable (*cf.* Water Lily), and also sepals and bracts (*cf.* Cacti). And bracts may grade into foliage leaves and behave like them. (Goebel, in his 'Organography', figures bracts of a *Phyllocactus* which have become pitcher-like, closely resembling a normal pitcher of *Sarracenia*.)

'Whatever may have been their origin, and whichever we regard as the parent form, surely the floral and foliage leaf have a common morphological value?'

Professor E. W. MACBRIDE said that he had listened to the paper with interest, and he might add with sympathy, for in zoology as in botany they had suffered in the past from the most divergent views as to the homologies between organs in different groups—homologies which, if accepted, implied irreconcilable theories as to the ancestry and evolutionary history of the animal phyla. When he was a student a number of influential biologists taught that vertebrates were derived from lobster-like creatures. The alimentary canal of the ancestor was supposed to have transformed itself into the spinal canal of the vertebrate, and the incipient vertebrate was credited with having invented a new alimentary canal from a groove on its belly. Still later the great group of Arthropoda, comprising four-fifths of the known species of animals, were supposed to have originated from Nematoda, thus cutting out from their family tree the segmented worms or Annelida which in so many fundamental characters agree with the Arthropoda.

Unless they could discover some criteria by which the true course of evolution could be detected it seemed hopeless to attempt to judge between these competing theories, because what one man considered likely another thought improbable, and *vice versâ*. About a year and a half ago, in a discourse delivered in the Royal Institution, he had endeavoured to set forth three cases in which the course of evolution could be followed without reasonable doubt, and by a study of these cases we could form a conception of the kinds of change that really went on; this change, when the evidence was complete, was always seen to be functional. These three cases were: (a) when a number of subspecies or local varieties of the same species were compared with one another; (b) when an animal in its development had free-living stages or larvae which gave a clue to the ancestral habits of the race; (c) when lineage series of fossils were available. Imaginary ancestral trees constructed by piecing together fossils drawn from different parts of the world were of no particular value, but in a lineage series fossils of the same kind of animal occurred in abundance in

some one locality, and could be traced through a vast series of overlying beds, and the slow and imperceptible change of structure correlated with an equally slow modification of habit and environment could be clearly made out. Unfortunately the early development of plants was embryonic, not larval, and so far as he was aware no lineage series of fossil plants were known. There remained, however, to botanists the comparison of local varieties and subspecies with one another, and from this evidence the kind of change which might be expected to occur in evolution might be discovered.

Dr. W. T. CALMAN said 'I have been much interested in listening to Dr. Hamshaw Thomas's remarks because many of the tendencies and problems with which he has dealt are common to present-day botany and zoology. Among the younger generation of zoologists, as among the botanists, we find a pre-occupation with physiology, a concentration on the activities of the present, and a lack of interest in phylogeny and in all that concerns the past, which reminds us of the sentiment enunciated in the words 'History is bunk'. As a result of this attitude there is a tendency among those zoologists who consider morphology at all to treat it very lightly, to gloss over the difficulties that surround the accepted interpretations, or to make these difficulties an excuse for abandoning the subject altogether.

'Almost the only group of zoologists to talk about phylogeny at the present day are the palaeontologists, and it is perhaps significant that many of the students of fossil animals seem to have arrived at conclusions very like some of those which Dr. Thomas has put before us to-night on behalf of the palaeobotanists. It is important to note among these conclusions an increasing admission of the part which parallel or convergent evolution must have played in phylogeny.

'There is one argument in favour of this conclusion which I do not remember to have seen stated, but which is at once suggested by Dr. Thomas's references to variation in members of a meristic series. I think it was W. K. Brooks who long ago pointed out that the resemblances between the successive limbs of an arthropod or the anterior and posterior limbs of a vertebrate could not be lightly dismissed with the statement that they were due to the fact that the members exhibiting them were homologous. Brooks pointed out, for instance, that the homology between the arm and the leg of a man was a relationship that dated back to the very beginnings of the vertebrate series; whereas many of the resemblances between these limbs concerned characters which had only appeared since the origin of the species *Homo sapiens*.

Similarly the homologies between the maxilliped and the walking-leg of a crayfish had their origin in the primitive arthropod if not in its annelid ancestor, but the similarities of structure which we regard as evidence of that homology are specific attributes of *Astacus*; in other words, the community of origin which we postulate to explain similarities in structure is really no more than an inheritance of the potentiality of developing similar characters.

‘But it is a commonplace of morphology that serial homology is of the same nature as homologies between different organisms, and the same argument that we apply to the successive limbs of the crayfish must be applicable to the resemblances between a crayfish and a cockroach. Here, again, resemblances in structure mean no more than the inheritance of the potentiality of assuming that structure under certain conditions; in other words, we have recognized the possibility of widespread, perhaps universal, parallelism and convergence in evolution, or, in Lankester’s words, ‘the principle of the plurality of causes tending to a common end’.

‘One of the most pressing problems of zoology at the present day seems to be to decide how far this process is to go. One zoologist, and so far as I know only one, has pushed it to its logical, if bitter, end. Professor Przibram, as I have elsewhere pointed out, carries the principle of parallel origin down to the smallest units with which the zoologist has to deal, and postulates the independent origin of all the species of Metazoa from separate species of Protozoa. If he is right Dr. Hamshaw Thomas and I will have to give up our hope that phylogeny can ever afford a basis for taxonomy—in fact, as far as we are concerned, ‘history is bunk’. I do not believe, however, that the prospect justifies such pessimism. As a systematist it seems to me incredible that the *Systema Naturae* should present the symmetrical aspect which it does unless structure were on the whole indicative of genetic affinity; and when the present-day phase of biological bolshevism has passed we may hope that a new generation of morphologists will take up the study of these problems very much in the spirit in which Dr. Hamshaw Thomas has dealt with them to-night.’

Miss E. R. SAUNDERS stated that regarding much of the matter dealt with by Dr. Thomas in his opening remarks she did not feel competent to express any opinion. She hoped, however, that his suggestion as to the need of coining a new terminology would not take practical shape in respect of the flowering plants until we had more definite evidence as to the stock from which they had originated.

In drawing comparisons between the fertile structures of

certain Pteridosperms and the male flower of *Populus* Dr. Thomas had confined himself to a description of the external form. She felt that to be on sure ground it was as essential for the botanist to study the vascular anatomy of the plant as it was for the zoologist to have knowledge of the skeleton in an animal. She understood that Dr. Thomas took the view that there was a fundamental difference between the morphological nature of the sterile members of the flower—the members of the perianth—and that of the fertile members—the stamens and carpels; that the sepals and petals were of the nature of leaves, but that he would regard stamens, at least in some unisexual male flowers, as comparable with stems. She thought that this conception was difficult to reconcile with many known facts. In illustration she might cite the following cases: the Water Lily, in which one found every gradation between the undoubted petal and the undoubted stamen; the variety of Sweet William in which the normal two whorls of five stamens were transformed into two whorls of five petals similar to those of the ordinary corolla; the strain of *Lobelia Erinus* in which it is sometimes the third, sometimes the fourth, sometimes the fifth floral whorl which becomes the staminal whorl, and in which individual stamens are often more or less petaloid. It appeared to her that Dr. Thomas's conception involved the division of the Angiosperms into two artificial classes, the one comprising those regarded as agreeing with the *Populus* type, the other, the rest.

Mr. G. C. ROBSON said he agreed with Dr. Thomas as to the insecurity of some of the morphological principles on which classification is based. He mentioned the difficulty often experienced in distinguishing likenesses due to genetic affinity from those arising from convergence. He briefly discussed the various criteria which have been proposed for the recognition of resemblances due to convergence.

[The Discussion on Dr. H. Hamshaw Thomas's paper 'The Old Morphology and the New' was continued at the General Meeting on 24 November 1932, as follows:—]

Dr. D. H. SCOTT in continuing the discussion said:

Dr. Hamshaw Thomas is a man who finds new things. His opening paper is based essentially on his own discoveries. He therefore has a better right to speak than the rest of us.

The rejection of phylogeny by some modern morphologists is, in a sense, justified. We can infer nothing from phylogeny, because phylogeny is unknown, 'a product of fantastic speculations' as Lotsy called it. To infer morphology from phylogeny is to put the cart before the horse.

Fossil plants must, of course, be used as well as recent plants in forming morphological conceptions. Their antiquity may give them the greater significance. This has long been recognized.

Lignier's theory of the origin of leaves (in megaphyllous plants) from modified thallus-branches is generally accepted and strongly supported by fossil evidence.

In Pteridosperms the reproductive organs are borne on appendages already fully differentiated as leaves. No doubt both the fertile and the sterile portions were once thallus-branches, but in Pteridosperms they have become obviously *foliar*. To call the fertile portions 'branches or branch systems' seems an anachronism! They were no longer that at the Pteridosperm stage.

Dr. Thomas tells us that in his Triassic seed-plants the seeds were borne on inflorescences, i.e., on axial organs. If so, were these plants Pteridosperms? This would involve the re-conversion of foliar into axial organs—the reverse of Lignier's process. Is there any probability of such an inverted change? All the same one must admit that the cupulate seeds of the Triassic plants look extraordinarily like some palaeozoic Pteridosperms.

On the main question, the morphology of the flower, I am in sympathy with Dr. Thomas's gallant attempt to bring it somehow into line with the fossils he has discovered: but the data are still inadequate.

Probably the oldest well-known true Angiospermous flower is Dr. Marie Stopes's *Cretovarium*. This Cretaceous petri-faction appears to be an ordinary flower of the Liliaceous type—there is nothing antique about it. It is a far cry from this to the Caytoniales or the Cycadeoids. As yet there is nothing in between; Darwin's 'abominable mystery' is as bad as ever!

The old carpellary theory, so well re-stated by Goebel in his great 'Organography', will probably continue to hold the field until more definite evidence can be brought against it.

Mr. W. C. WORSDELL said that he considered the Pteridospermous sporophyll as the probable ancestor of all modern foliar organs in the Phanerogams. Many of the palaeozoic forms cited by Dr. Thomas are merely variants of this ancient sporophyll.

As against Dr. Thomas's view that many of the reproductive structures in modern Angiosperms and Gymnosperms, especially those 'sporophylls' which bear terminal sporangia, are primitive, he held that it is much more probable that such structures are descended from a more complex type of sporophyll; excessive reduction in the course of evolution has

resulted in the production of apparently simple structures which simulate primitive types, and botanists have been misled into supposing that these represent the primeval forms; examples of this phenomenon are seen in the sporophylls of *Ginkgo*, ovules of *Gnetum* and *Podocarpus*, seminiferous scale of Abietineae, stamen of Angiosperms. In Cycads the female sporophylls of the majority of genera have almost certainly been derived from the more complex type of *Cycas*. In Abietineae abnormalities show that the apparently simple structure of the seminiferous scale has been derived from a much more complex one, viz. a sporophyll-bearing axillary shoot. The stamen of the Angiosperms bearing sporangia terminal to a filament, far from being a primitive structure, and of the nature of a branch, has probably been greatly reduced from a more complex sporophyll. As every transitional form is known between stamens and foliage leaves, it follows that the two represent homologous structures. If, on recent views, the stamen is to be regarded as a branch, then he would have none of the New Morphology, but would subscribe himself an old morphologist.

Mr. J. PARKIN said that, accepting the view that the large fern-like leaf has arisen from the limitation in growth of an arm of a forking thallus, on *à priori* grounds it could be advanced that in one or more lines of descent the reproductive-bearing branches of the original thallus became segregated from the assimilating ones before these latter assumed the form of foliage leaves. In such an event it would be morphologically incorrect to homologize modifications of these reproductive branches with foliar organs. This, he understood, is Dr. Hamshaw Thomas's contention.

On endorsing his view that the Angiosperms may have descended from the Pteridosperms, there, however, seems to be inadequate grounds for thinking that in this great plexus the sporophylls were originally differentiated apart from the foliage leaves; so there does not appear to be a clear case for regarding stamens and carpels as other than modified leaf-structures.

At the same time, seeing we know nothing of the past evolutionary history of these organs, it may be of advantage to study them in the light of the 'New Morphology', even if it may lead to a *reductio ad absurdum*.

A cupular origin of the carpel is at least suggestive, and may be worth exploring.

In reply to a remark by the President, Mr. J. RAMSBOTTOM said he did not know whether he could be regarded either as an old or a new morphologist. He hoped, however, he

would please both by a quotation from Darwin concerning morphology: 'This is one of the most interesting departments of natural history, and may almost be said to be its very soul'.

Dr. Thomas in his interesting paper had concerned himself mainly with the equivalence of structures found in flowering plants, and in pointing out some of the difficulties of the classical interpretations.

Asa Gray, in his 'Structural Botany', defines morphology as follows:—'Morphology, the doctrine of forms, as the name denotes, is used in natural history in nearly the same sense as the older term Comparative Anatomy. If it were concerned merely with the description and classification of shapes and modifications, it would amount to little more than glossology and organography. But it deals with these from a peculiar point of view, and under the idea of unity of plan or type'.

What significance is to be placed on the expression 'unity of plan or type' in so far as it relates to botanical morphology? Is it not a relic of the period when every species was thought to be a special creation? Unity of plan then explained similarities, and, moreover, lead to such fundamental discoveries that even to-day there is general reluctance to think of an organ *sui generis*. Are we not still pushing the idea too far? It seems necessary to consider the whole of the vegetable kingdom. Then, taking the old assumption of special creation, it would task the imagination of modern botanists even to suggest any unity of plan in many groups of Cryptogams, though it may be pointed out that Micheli and others found 'flowers' in Agarics. On the other hand, considering the matter from the standpoint of evolution we must admit that any unity of plan on the classical scheme came into play comparatively late. Some hypothetical archegoniate green alga presumably had the potentialities of stem, root, and leaf, but is it logical to assume that these are the only organs that could develop or have developed?

If such a plan is found sufficient for our purpose it would be unscientific to add to it, but so it would be to twist the facts of development to fit in with an old philosophy.

One of the special points in Dr. Thomas's paper was the suggestion of a polyphyletic origin of the angiospermic flower, mainly on the basis of the stamen. How is the general similarity of the embryo sac explained? It may perhaps be considered as due to similarity in independent reduction of the female prothallus, but the triple nuclear fusions leading to endosperm formation would seem so peculiar as to have great weight in arriving at any conclusion.

If substantial reasons can be brought forward to show that the angiospermic embryo-sac has arisen several times

mycologists probably will feel less certain that the ascus can be regarded as a criterion of monophyletic development.

Mr. ERIC ASHBY said that if the New Morphology is to enlist the work of physiologists and geneticists the morphologists must be quite clear as to what significance is to be attached to 'evolutionary trends'. To fit these trends into the geneticists' system of evolution they must be endowed with 'survival value'. It is significant that the majority of the most important evolutionary trends have no obvious survival value, and are indeed notoriously independent of the environment; one has only to instance centripetal and centrifugal wood, reduction of prothallial cells in the male gametophyte of Gymnosperms, and the fusion of parts in Angiosperms. To postulate a slight survival value to such trends is to assume what the morphologist sets out to prove. The alternative suggestion is that there have been changes in the germ-cells, independent of environment, and common to many unrelated phyla.

Dr. MARGARET J. BENSON said that she was prepared to accept Bower's delightful monosyllabic definition of morphology, that it deals with 'how in the past plants came to be such as we now see them'.

In this quest the results of palaeobotany are as helpful as signposts. The inadequacy of these results in the case of the phylogeny of Angiosperms is notorious, but Dr. Hamshaw Thomas is doing a Herculean task in not only securing new Mesozoic specimens, but in the very difficult and delicate work of treating these in the laboratory when brought in from the field. He now asks us, on the strength of these discoveries, to discard some of the older conceptions as to the morphology of the reproductive structures of Angiosperms. He shows that the newly described Mesozoic Angiosperms show reproductive structures difficult to bring under the old category of leaf—whether carpellary or staminal.

Her contribution to this discussion is to refer to the classical work of Solms-Laubach on the anatomy of *Cycas*, a genus most nearly of all existing genera approximating to the Carboniferous Pteridosperms. Solms-Laubach showed that the seed 'leaves' in *Cycas* are borne in all respects as the foliage leaves, and that the axis of the strobilus is absolutely continuous with the main axis of the plant. This was doubtless the case in the Pteridosperm, and she deduced, therefore, that we cannot give up the leaf theory of the homology of the carpel and stamen. She suggested that the new discoveries of Mesozoic floral structures could be explained by taking into account the well-known phenomenon of the sporangiophore or support of the sporange, which varies in length but is

probably always potentially present. This body, with its sporange, whether half anther or seed, undoubtedly is exceptionally plastic, and may be regarded as a last outpost of the primitive thalloid plant.

Dr. Thomas could also safely refer some of the new forms to the widely illustrated phenomena of reduction and fusion of leaves. She concluded therefore that there is so far no necessity to regard the reproductive structures of Angiosperms as axial in origin.

Dr. T. A. SPRAGUE agreed with the author and Mr. Worsdell that evolution in the Angiosperms was largely a story of reduction, not only in the flower, but also in the foliage leaf, the compound leaf being apparently a primitive type relatively to the simple one. It seemed to him that some of the old morphological concepts were too rigid, and that certain distinctions commonly drawn between one morphological type and another lacked reality, e.g., the distinction between compound and simple leaves. The distribution of types of foliage leaf in the Dicotyledons suggests that there is a more essential difference between the divided leaf (compound or lobed) and the undivided leaf than between the compound and simple types. In numerous groups, e.g., Malvales, Araliaceae, and Umbelliferae, the palmate and palmatifid (or pinnate and pinnatifid) types are intimately associated, sometimes in the same genus, so that their evolutionary connection is evidently very close. Many other families, e.g., Annonaceae, Lauraceae, Apocynaceae, have exclusively undivided leaves.

The entities affected by evolution are the living organs and tissues, and not the morphological concepts by which we seek to precise them. The differentiation of root, stem, and leaf acquired by the Angiosperms has been lost to a certain extent in some aquatic groups, e.g., *Utricularia* and Podostemaceae, and in some parasites, e.g., Rafflesiaceae. Similarly the distinction between the axial and foliar parts of a flower, which is easily traceable in the hypogynous type, is lost to a certain extent in the epigynous flower, the tissues surrounding the ovary in the latter being frequently quite undifferentiated from it.

Dr. HAMSHAW THOMAS, in replying to Miss Saunders, said he agreed with her view of the importance of studying vascular structure; he had tried to show that the distinction between leaves and lateral branches was probably an arbitrary one. On the hypothesis that the stamens represented lateral branches and that foliage leaves and petals were derived from branch systems, no difficulty was presented by the apparent transformation of stamens to petals, and there was no need to regard this as a reversion.

In replying to other speakers, he said that use of the term leaf implied a flattened organ well adapted for photosynthesis. The fertile leaf of a pteridosperm was regarded as derived from a branch system in which the lower branches were generally modified to expanded photosynthetic pinnules, while the tips of certain segments retained their original character and were fertile. In other cases the lower branches of the frond were probably fertile and little modified while the upper branches were flattened and aggregated. In replying to Mr. Worsdell he considered that nothing could be gained by the adoption of the agnostic attitude. We should instead try to set out the knowledge already gained and draw a provisional picture. This would show where more knowledge was needed, and we could concentrate on trying to fill up the blank spaces in our picture. It may well happen that in the light of new knowledge our picture would prove to be incorrect; then we should commence again, with a rearrangement of the data. It could perhaps be argued that forms like *Ginkgo*, *Gnetum*, and the Podocarps possessed greatly reduced seed-bearing structures, but if the arguments for and against this view were set out and examined without prejudice, the balance of argument seemed in favour of their being primitive types of structure. It was valuable to find a general agreement on the idea that evidence of reduction was to be found in all groups, since the speaker had placed considerable reliance on that view.

The Botanical Secretary had pointed out the really weak spot in the argument for the polyphyletic origin of the Angiosperms. We knew little or nothing about the embryo sacs of the Pteridosperms, but it was not impossible that the Angiospermic type of embryo sac was evolved in this group in late Palaeozoic times. Dr. Ashby had raised a most important and fundamental point, which should be carefully considered by all morphologists.

In summing up, it seemed that a general survey of all land plants, excluding flowering plants, provided strong evidence for the derivation of large leaves and reproductive parts (sporophylls) from branch systems. It followed that *either* the leaves, stamens, and carpels of Angiosperms have been evolved from similar branching structures, *or* that the flowering plants had arisen from independent algal ancestors, as suggested by Prof. Paul Bertrand, and had passed through a series of evolutionary stages with incredible rapidity without leaving any trace in our fossil floras. The speaker considered it more reasonable to derive the Angiosperms from Gymnospermous types, and these from types resembling known Pteridophytes. In this case compound leaves and branched stamens are *either* primitive *or* have been derived from simple forms by a reversal of the course of evolution—for which no evidence

existed. The fact that we know so little about the phylogeny of the Angiosperms is no reason for refusing to face this problem. Its solution does not depend on the production of a complete scheme of flowering plant phylogeny. Our knowledge may be incomplete, but it is our duty to make sure from time to time that our general ideas of plant evolution agree as closely as possible with the information we possess.

24 NOVEMBER 1932

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 10 November 1932, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted:—Martin Audley Foquett Sutton.

Certificates of recommendation of the following candidates for Fellowship were read:—For the second time, in favour of Richard Frederic Nevill Aldrich-Blake; for the first time, in favour of Frère Marie-Victorin, Rubugunde Madhava Row, Norah Lillian Penston, and Robert Henry Corstorphine.

The President announced that the Council will shortly be considering recommendations for an Associate (zoological) to fill the vacancy caused by the death of Mr. Andrew Scott.

J. G. Koenig's manuscripts and herbarium.
By Dr. A. B. Rendle.

JOHN GERHARD KOENIG, a native of Courland, was a pupil of Linnaeus, who dedicated to him the genus *Koenigia*. collected by Koenig in Iceland, which he visited in 1765. Many other species found by Koenig on this visit are described by Linnaeus in the 'Mantissa' (1767) and the specimens are in the Linnean Herbarium. In 1768 Koenig went to India as Surgeon and Naturalist to the Danish Settlement at Tranquebar. In 1774 he entered the service of the Nawab of Arcot, and in 1778 was appointed Naturalist on the Madras establishment of the H. E. I. C. He died in 1785, bequeathing

his herbarium and manuscripts to Sir Joseph Banks. The MSS. were arranged and indexed by Banks's librarian Dryander, and were bound in nineteen volumes. The extensive herbarium contained many new genera and species from India and Ceylon. The specimens are generous, well-mounted, and often annotated by Koenig. The manuscripts contain very full descriptions of the plants as well as notes on animals and minerals collected and on plants of medicinal value; also journals, notably of his voyage to Malacca and Siam (1778-9). Koenig sent specimens during his life to Banks and Solander and to other European botanists, including the elder and younger Linnaeus, who published descriptions of many of his species in the 'Mantissa' and 'Supplementum' respectively. Another recipient was Prof. Retzius of Lund, who described many of Koenig's discoveries in the various parts of his 'Observationes Botanicae' (1781-91). With the MSS. have been incorporated letters from Koenig to Solander, a fellow-pupil under Linnaeus, and to Banks.

The habits of the Pycnogonida.

By Dr. Isabella Gordon.

FEEDING habits of the adults.—Several species with long chelophores have been observed feeding on various Hydrozoa. The polyp-cup is seized by the stalk and pressed to the mouth while the polyp is being devoured. *Phoxichilidium* has been described as tearing off a bunch of tentacles of *Lucernaria*—a sessile medusa—and pressing the torn end to the mouth. *Pycnogonum*, which has no chelophores in the adult stage, anchors itself to a sea-anemone, plunges its proboscis far into the tissues and sucks the juices.

Habits of the larvae.—In the majority of Pycnogonida the male takes charge of the eggs, carrying them on the ovigers until the larvae hatch out or, in extreme cases, until they have assumed most of the adult characters. Many larvae are known to lead an independent existence at a comparatively early stage. The majority of these feed on Hydrozoa either ecto- or endo-parasitically. Still others feed on Holothuria, on the sea-slug *Aplysia*, or on a pelagic nudibranch mollusc. In 1927 Ohshima described a new Japanese form found living within the shell of an edible bivalve mollusc. In this connection reference was made to an apparently erroneous statement contained in one of J. G. Koenig's letters to Linnaeus namely, that a species of Pycnogonid 'bores through the shells of molluscs and sucks their juices'.

Pelagic occurrence of Pycnogonida.—Larvae are occasionally found clinging to or living within swimming-bells of various Hydrozoa. Numerous specimens, both larval and adult,

have in certain years been carried on sea-weed by ocean currents and winds from the Sargasso Sea to Cape Cod. Fage has recently described a distinct pelagic phase for *Nymphon gracile* coinciding roughly with the breeding-season ; specimens are found at the surface from November to June, the numbers reaching a maximum in February and March ; ovigerous males preponderate in the first, females in the second half of the period.

In conclusion, reference was made to the possibility of the so-called ovigers possessing some function other than that of egg-bearing, at any rate in those forms in which they are well developed in both sexes. In *Colossendeis* and *Decolopoda* they are large in both sexes and show considerable signs of wear in older specimens, yet no egg-bearing male has as yet been observed.

Professor E. W. MACBRIDE asked whether it was correct to say that the male ceased to swim when the developing eggs and larvae became too heavy, since there would be no increase in weight.

Mr. R. H. BURNE asked whether it would be possible for small Pycnogonida to enter mussel-shells by means of the siphon.

Dr. W. T. CALMAN pointed out that, while the increase in weight during early development might not be great, the larvae become much more cumbersome with increase in size.

Dr. GORDON, in reply, stated that there would not be any difficulty about their entering mussel-shells—the pea-crab, for example, does so frequently—but it appears that, with the exception of the Japanese form mentioned, they never do so, and the occasional association of Pycnogonids with mussels is, as a rule, quite fortuitous. Also, the number of egg-masses acquired by the male may increase to six or even eight ; but it is probably important for the larvae that they should hatch out on the sea-floor, where their future supply of food would be.

The Discussion on Dr. H. Hamshaw Thomas's paper 'The Old Morphology and the New' was continued. (See pp. 39-46.)

The following paper was read in title :—

‘The habits and feeding mechanism of the Amphipod
Haustorius arenarius Slabber.’ By RALPH DENNELL.

8 DECEMBER 1932

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 24 November 1932, having been circulated, were taken as read and confirmed.

The President reported the death of Frederick William Lucas, Fellow of the Society.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Frère Marie-Victorin, Rubugunde Madhava Row, Norah Lillian Penston, and Robert Henry Corstorphine.

The following candidates were balloted for and elected as Fellows :—Irene Alexandra Francis Hilton, M.Sc. ; Kurumthottical Cherian Jacob ; Thomas Kenneth Rees, M.Sc. ; Mohamed Eweis, B.Sc. ; William Charles Osman Hill, M.D., Ch.B. ; Abbas Fathi El-Helaly, B.Sc. ; John Hugh Davie, B.Sc. ; Chrystabel Prudence Goldsmith Procter ; John Vardy ; Reginald Edward Vaughan, B.Sc. ; Harold Alexander Wootton, B.Sc. ; and Richard Frederic Nevill Aldrich-Blake, M.A.

The Origin and Genetics of the Garden Dahlia.

By Mr. W. J. C. Lawrence.

THE origin of many cultivated plants is obscure and their relation to other species of the genus often uncertain. The problem of the origin of the Garden Dahlia (*D. variabilis*) is typical. Introduced into Europe from Mexico in 1789 it rapidly began to vary, showing a great range of form, size, and colour. Since the other *Dahlia* species show little variation, there has been much speculation as to the origin and variability of the Garden Dahlia.

Issued 17 May 1933.]

As the result of experiments made at the John Innes Horticultural Institution, a solution to the problem can now be tentatively advanced. The results of the investigations are, briefly, as follows :—

(1) With the exception of *D. variabilis*, *Dahlia* species may be divided into two groups for flower colour—Group I with magenta or ivory flowers, Group II with scarlet or yellow flowers. *D. variabilis* combines the colours of both groups, an observation which suggested it might be a hybrid between members of the two groups.

(2) The Garden Dahlia is found to have twice as many chromosomes as the other species—a phenomenon often associated with the successful hybridisation of species.

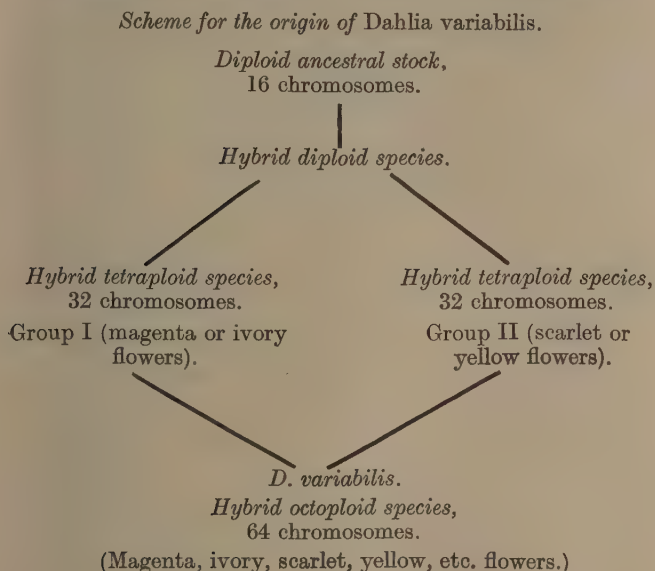
(3) Further, the behaviour of the chromosomes at meiosis not only shows that *D. variabilis* is a hybrid octoploid species, but also shows the *kind* of hybrid it is. Primary and secondary association of the chromosomes clearly indicate that it is a *hybrid* octoploid which has arisen from the crossing of *hybrid* tetraploid species.

The genetics of flower colour in *D. variabilis* lend strong support to this view. It is characteristic of hybrid polyploids that many of the genes will be in duplicate or that pairs of similar genes will occur, since the parent species must have been identical in some respects, but somewhat different in others. Thus in the Garden Dahlia the genes producing flower colour are in duplicate, two for flavone colour (called *I* for ivory and *Y* for yellow) and two for anthocyanin intensity (called *A* for pale and *B* for deep pigmentation). Presumably the genes *A* and *I* were contributed by the Group I parent with magenta (pale) or ivory flowers, and the genes *B* and *Y* by the Group II parent with scarlet (deep) or yellow flowers, since the two flower colour groups are distinguished by precisely the same differences. Further, each of these four colour genes is represented four times; and their inheritance is tetrasomic, indicating the tetraploid nature of the parents of *D. variabilis*.

It is now apparent why the Garden Dahlia is so variable. (1) It is a hybrid between hybrids, and therefore combines many differences. (2) It is a high polyploid, probably with many duplicate or similar genes, each of which is represented, not twice as in a simple diploid plant, but from four to eight times. The result of this is a vastly greater number of possible gene combinations with a correspondingly greater range of variations. (3) The genus is self-sterile. Cross-fertilisation is therefore enforced and the Garden Dahlia is maintained in a complex heterozygous condition and cannot breed true. (4) The Garden Dahlia has been domesticated in Mexico for

many centuries, and semi-double forms were actually described and figured by a Spaniard living in Mexico in 1575. Hence the plants introduced into Europe in 1789 were only varieties of a species already long established and widely varying. (5) In other words, *D. variabilis* combines the results of specific differentiation with a high degree of polyploidy—a constitution which is found in many of our most important cultivated plants.

The scheme for the origin of *D. variabilis* is given below :—



The significance of the present study lies not so much in the immediate results obtained as in the illustration it provides of the combined technique of morphology and cyto-genetics which is coming to be of such importance in the analysis of complex species.

In answer to a question by the President the lecturer said that a number of genera are known in which only the polyploid species now exist, the presumed earlier diploid forms having become extinct. *Verbascum*, *Digitalis*, *Pyrus*, *Saccharum*, and *Betula* are examples.

Variation in *Antirrhinum*. By Dr. B. Barnes.

DURING the past few years, some peculiar forms of the garden Snapdragon have been noticed.

Form 1.—Three plants developed in 1930 from seed of a mixed stock. The plants were of rather weak growth, with narrow leaves and a general elongated habit. Flowers were produced freely, all abnormal and all of uniform character. The calyx was slightly modified, being nearly regular and almost or quite polysepalous. The corolla consisted of five (rarely four) free sepal-like segments, and was never personate. Good stamens never developed, the androecium being represented by small rudiments, without a vascular supply. The gynaecium was strongly modified. Five carpels were usually present, and their loculi were open above, communicating with a massive hollow tube formed of five united styles. In some flowers the placentas were axile below and parietal above, then springing from the side of the styler tube: in others, axile placentas alone occurred.

Selfing was impossible, as pollen was not formed, and attempts at crossing with normal flowers always failed. The carpels ultimately withered; seeds did not mature.

The plants of Form 1, and cuttings from them, died during the winter of 1931–32.

Form 2.—A single plant bearing green flowers was obtained from a garden in Sussex in 1929. The stock has since been kept in cultivation at the Chelsea Physic Garden by the kindness of Mr. Hales. The vegetative characters of this form do not differ from those of normal plants in any important respect.

The calyx is not specially peculiar. The corolla consists of five green irregular segments, sometimes all free, sometimes showing casual unions, and sometimes vaguely united into two lips: a personate corolla has not been seen. Ordinary stamens are always absent, the androecium being replaced by four subsidiary open carpels, with ovules borne on placentas lying on the inner and outer surfaces of the carpels. Similar carpel-stamens are well known in garden stocks of *Sempervivum tectorum*, and comparable structures are under investigation in a plant of *Delphinium elatum*. Staminodes of greater or less complexity are often present in the green-flowered *Antirrhinum*, in the posterior position.

Plants of this form have never set seed, and crosses with normal plants have not been obtained.

Form 3.—A single plant of Form 3 was noted in 1931. The vegetative characters and the general form of the flowers are quite normal, but many of the flowers have developed additional petaloid structures. Usually, one or two of these structures have appeared in the posterior position (that is,

in the place of the theoretical fifth stamen), but occasionally similar appendages have arisen from the bases of some or all of the normal stamens of the flowers. The abnormal characters of Form 3 are not so constant or extreme as those of Forms 1 and 2.

Mr. E. ASHBY asked what was the anatomy of the flowers with an appendage.

Mr. F. W. JANE said that he had not met with similar abnormal ovaries in this species, but had occasionally found trilocular ovaries. Quadrilocular ovaries had been observed in *Lindenbergia grandiflora*, but not in *Antirrhinum majus*. In some *Antirrhinums* bred by Messrs. Sutton & Sons, Ltd., some of the ovaries had free central placentation. With regard to the staminal outgrowths mentioned, the stamen sometimes bore a single outgrowth from the base of the filament in the flowers which he had examined, and sometimes there was one on each side. A well-defined vascular strand ran up the filament, and much smaller vascular strands entered the outgrowths. The outgrowths were never fertile, and varied from small teeth to large petaloid structures. Even when the stamen was sterile, and much reduced in size, it still received the main vascular strand.

Professor R. R. GATES remarked that Dr. Erwin Baur and his colleagues had produced a remarkable series of factor mutations in *Antirrhinum*, some of them showing similarities to the form described by Dr. Barnes, by treatment of the seedlings with X-rays and also with various chemicals. These included not only striking changes in habit and in foliage, but also in flower characters, as indicated by such names as *muscoides*, *angustifolia*, *choripetala*, *fimbriata*, *fistulata*, *centroradialis*, and *neohemiradialis*.

Dr. BARNES replied that he had avoided any detailed anatomical description because he had a student working on the anatomy and did not wish to anticipate her results.

With regard to carpel number: of 75 flowers of which records were kept, 74 had five and one had six carpels. He was familiar with Professor Baur's work, but he had not mentioned it because he was solely concerned with the morphology of the abnormal plants, and no suggestion as to their manner of origin was discussed.

The Olduvai (Tanganyika Territory) Expedition, 1931.

By Mr. A. Tindell Hopwood.

THE Olduvai Expedition of 1931 was undertaken with a view to gathering fresh evidence concerning the human skeleton found there in 1913 by Professor Hans Reck, of Berlin.

Additional objects were the formation of collections of such stone tools as might be present in the deposits and to obtain natural history specimens, especially fossil mammals, for the British Museum (Natural History). In all three branches the expedition was completely successful, although the significance of the evidence regarding the human remains was not fully realised for some time after the return of the Expedition.

Olduvai is a deep gorge cut into the eastern margin of the Serengeti. Its mouth lies in lat. 3° S., long. $35^{\circ} 25'$ E., and it extends in an approximately S.E.-N.W. direction for nearly twenty miles. To the north lies the dissected table-land of the Sonjoo Hills, to the east the highlands of the Giant Cauldrons (a complex of extinct volcanoes with large subsidence-craters), to the south the extinct volcano of Lemagrut and the Serengeti, to the west the Serengeti extends to Lake Victoria. The rainfall is scanty and often fails, hence the country is semi-desert.

The vegetation is composed of xerophytic grasses, stunted Acacias of two genera, *Sanseveria*, and plants resembling *Sarcostemma*. As the small rains approached, the Acacias threw out a few leaves and occasional spikes of bloom. The colour of the bark appeared to become lighter and more silvery. The rain was limited to two or three light showers, so that the plant-life had no stimulus to develop to its full extent. On the mountains were forests of Umbrella Acacias, shrubby Malvaceae, and a number of deciduous trees. The springs often had ferns similar to the European Maidenhair Fern growing in crevices round the cliffs from which the water dripped.

Owing to the drought and to the ravages of locusts, the game kept far to the westward. The species seen on the plains were *Bubalis cokei*, *Gorgon taurinus*, *Rhynchotragus* sp., *Gazella thomsoni*, *G. granti*, *Giraffa* sp., *Equus quagga* subsp., and *Diceros bicornis*. In the gorge were *Oreotragus* sp., *Rhynchotragus* sp., *Diceros bicornis*, and *Procavia* sp. On the mountains we found *Aepyceros melampus*, *Taurotragus oryx*, *Giraffa* sp., and *Diceros bicornis*; *Elephas* was reported in some Bamboo Forest about twenty miles away. Lion and Leopard were generally distributed, but on the plains and in the gorge were Spotted Hyaena, Jackal, and Bat-eared Fox. At different times Spotted Genets and Wild Cats were seen.

The most important fossils were *Deinotherium* found associated with *Palaeoloxodon antiquus recki*, and *Hipparion* associated with *Equus* sp. (probably *Dolichohippus grévyi*).

Subsequent work by Professor P. G. H. Boswell, F.R.S., has disproved the theory that the human remains were of Middle Pleistocene age, and shown that they cannot be earlier than the Upper Pleistocene.

Over 1500 stone tools were collected from well-defined horizon. They cover all types from pre-Chellean to Mousterian.

Mr. H. N. RIDLEY stated that the swarming of bees round the radiator of the car mentioned by Mr. Hopwood might be attributed to the oil or the perspiration of the occupants, as in his Pahang expedition bees swarmed all over the explorers for the sake of the perspiration. Dragonflies appearing in flights in the dry deserts of Olduvai were paralleled by the flights arriving at Christmas Island, believed to be from Australia, a distance of 1100 miles, though there is no breeding-place there for these insects.

Dr. J. BURTT DAVY said that the pendulous, succulent, leafless shrub with latex, shown in Mr. Hopwood's photograph as a nesting-place for weaver-birds, is probably *Sarco-stemma viminale* (L.) R. Br., of the family Asclepiadaceae. This plant is variable in habit in different habitats, sometimes forming a bush with woody stem and succulent branchlets; sometimes (as when growing on slopes or banks) it is pendulous; sometimes it scrambles over other bushes; it is even said to 'twine,' though he had never seen it behaving in this way. It is markedly xerophytic. The species is widely distributed in Africa, from Eritrea through east tropical Africa to the Cape Province (as far west as the Keurbooms River), and from the French Sudan to the drier parts of the 'Western Province' of the old Cape Colony.

The other succulent shown on the slides is an Aloe; it would be unsafe to suggest a specific name, as fifty or more species are known from tropical Africa.

Mr. G. TANDY and the PRESIDENT added some comments, and Mr. Hopwood replied.

The following papers were read in title :—

Scientific Results of the Cambridge Expedition to the East African Lakes, 1930-1.—8. Hydracarina. By O. LUNDBLAD.

—— 9. Leeches. By J. PERCY MOORE.

—— 10. On some aquatic Coleopterous Larvae. By A. D. IMMS.

5 JANUARY 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 8 December 1932, having been circulated, were taken as read and confirmed.

The PRESIDENT exhibited the vellum sheet with the signature of HIS IMPERIAL MAJESTY THE EMPEROR OF JAPAN as an Honorary Member of the Society, which had just been received, together with the following explanation of the design surrounding the Imperial autograph :—

‘The design around the Imperial autograph represents the entwined branches of *Chrysanthemum* and *Paulownia*, the emblems of the Japanese Imperial Family, crowned with the Imperial crest between two phoenixes. The ribbon is of Wungen-Nishiki, or literally halo-brocade, for in the pattern stripes are graduated like a halo round the sun. Wungen-Nishiki has been used as border of the mat for the Throne from ancient times. No subject in Japan has ever been allowed to sit on a Wungen-bordered mat. The particular ribbon, for this reason, seems full of meaning to be put under the Imperial autograph in the design.’

The PRESIDENT made an announcement calling special attention to the opening of the Library between 5.0 and 6.0 p.m. on Wednesday evenings.

The PRESIDENT announced that there was a vacancy in the list of Associates by the death of Mr. Herbert C. Chadwick.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—Norman Woodhead, John Hugh Davie, Thomas Kenneth Rees, George Arthur Nelson, and Richard Frederic Nevill Aldrich-Blake.

A certificate of recommendation of the following candidate for Fellowship was read :—For the first time, in favour of Leslie John Walker.

The homes of The Linnean Society of London. By Mr. S. Savage, Libr.L.S.

It is remarkable that the meetings of our Society, throughout the hundred and forty-five years of its existence, have all been held within half a mile of the spot where it was founded ; and an area bounded on the north by Oxford Street, on the east by Charing Cross Road, on the south by Piccadilly and the north side of Leicester Square, and on the west by Old and New Bond Streets, contained the seven buildings which in succession were the scenes of its activities. During the past summer several photographs have been specially taken





of those buildings which still survive; and these, together with other records, are reproduced in the accompanying Plate. The information gathered concerning the various homes of the Society is condensed under the following headings arranged in chronological sequence:—

Marlborough Coffee House, Great Marlborough Street.—The foundation meeting took place in this Coffee House on 26 February 1788, when seven persons attended—Dr. James Edward Smith (first President), the Rev. Samuel Goodenough, afterwards Bishop of Carlisle (first Treasurer), Thomas Marsham (first Secretary), Jonas Dryander (first Librarian), James Dickson, John Beckwith, and John Timothy Swainson. A second meeting was held in the same place on 18 March 1788. The place of these meetings was no doubt determined by Smith, who, at the time the Society was founded was about to remove from No. 14 Paradise Row, Chelsea (now a part of Royal Hospital Road), to No. 12 Great Marlborough Street. Up to the present I have failed to trace a picture of the Marlborough Coffee House.

No. 12 Great Marlborough Street.—At the fourth ‘Fellows’ Meeting (in distinction to ‘General’ Meetings), held on 20 May 1788, it was resolved to ask the President, in whose house the first General Meeting had been held on 8 April 1788, to allow the Society to have two rooms at a nominal rent of £20 per annum; the second room to be used as the Society’s library. This was agreed to, and for the next seven years the Society continued to meet in its President’s house, which contained the Linnean Collections purchased by him in 1784. About September 1795 Smith removed to a house in the Vineyard, Hammersmith, and the Society had to seek new quarters.

No. 12 Great Marlborough Street, a typical example of an early Georgian town house, remains to-day practically unchanged (Pl. 1. fig. 1). The founder of a firm of solicitors, Messrs. Broughton, Holt & Middlemist, now occupying it, obtained possession in 1796. Flanked by tall modern buildings, it is a remarkable survival.

No. 10 Panton Square.—From 1795 to 1805 the Society occupied this building jointly with the Westminster Subscription Library, whose librarian, Benjamin Price, became also the Society’s Librarian. The house consisted of cellars, ground and first and second floors. The Society appears to have occupied the first floor. Panton Square (or Panton Yard, as it was first called) was built by Colonel Thomas Panton on ground purchased by him in 1664 with money obtained as proprietor of a gambling hell known as Piccadilly Hall. He also built Panton Street off the Haymarket—which should not be confused with Panton Square. Early

maps show Panton Square as several small squares or yards connected by a narrow road, but at the time the Society had its home there it was a *cul-de-sac*, only the first yard surviving. In 1868 the name Panton Square was abolished and it became part of Arundel Street, which connected it with Coventry Street. In 1923 the whole site was covered by an extension of Messrs. Lyons's Coventry Street 'Corner House.' So far, attempts to obtain a picture of No. 10 Panton Square have been unsuccessful, but a water-colour drawing of the Square, painted by T. Hosmer Shepherd before 1850, now in the Crace Collection in the British Museum, no doubt gives some idea of what it looked like when the Society met there (Pl. 1, fig. 2).

No. 9 Gerrard Street, Soho.—In 1805 the Society decided to remove from Panton Square, which had been its home when it was incorporated by Royal Charter in 1802. With No. 9 Gerrard Street (Pl. 1, fig. 3) the Society for the first time occupied a 'House' in the full sense, and remained in possession of it for sixteen years. This house is believed to have been previously the Turk's Head Tavern, and certainly its exterior supports that tradition. (This Tavern was much frequented by Dr. Samuel Johnson, and it was here that he and Sir Joshua Reynolds founded the Literary Club in the year 1764.) The Society's occupation of this building was followed by that of the Westminster General Dispensary, which institution has record of its occupation from the year 1826. Although in March 1815 the Society had entered upon a new lease for nine years, the opportunity of transferring to better quarters was not neglected, and in 1821 the Anniversary Meeting was held in Soho Square.

No. 32 Soho Square.—By an arrangement with Robert Brown (Librarian, 1805–1822; President, 1849–1853), the Society undertook to lease part of this handsome building (Pl. 1, fig. 4) that had been Sir Joseph Banks's town house from the autumn of 1777 till his death in 1820—Brown himself occupying the rear portion, which had an entrance in Dean Street*. Although its visible frontage in Soho Square is small, it represents only one-third of the real frontage, which extends to the left. The interior has some fine ceilings, including a lofty arched one of unusual design, and an exquisite overmantel and fireplace in one room. The Society remained in this house for thirty-six years, until 1857, when it removed to Old Burlington House. In 1852, No. 32 Soho Square was exempted from Poor Rate, on account of its being used for 'purposes of science.' Until recent years the building

* Beresford Chancellor, 'The Squares of London,' 1907, is incorrect in stating that Sir James E. Smith occupied Banks's house after his death.

was occupied by the Hospital for Diseases of the Heart, but at the present time is in possession of Messrs. Thornton-Smith Ltd., a firm of interior decorators. The wall-tablet commemorating Sir Joseph Banks was fixed in 1911.

Old Burlington House.—From time to time the Society had petitioned the Government for accommodation suitable for its needs. For instance, in 1849 the President was requested to make application to the Government for the grant of the house in Craig's Court, Whitehall, that was about to be vacated by the Museum of Economic Geology. Although nothing came of that application, events happened in the next few years that made it possible later on for our Society to become the Crown tenant of a building specially built for its needs. In 1852 Robert Brown, then President, attended a meeting of the Council of the Royal Society, at which the Presidents of the Geological, Astronomical, and Chemical Societies were also present, to consider a memorandum drawn up by the Earl of Rosse, Pres. Roy. Soc., recommending to the Government the bringing together of the London scientific societies under one roof, but leaving to each society its independent action. In the same year it was reported that ground had been purchased at Kensington Gore for that purpose; but as this site did not meet with the approval of the Societies interested, they petitioned for a more central locality. In 1854, on the purchase of Burlington House by the Government, the President (Thomas Bell), the late President (Robert Brown), the Treasurer, and the Secretary were appointed a deputation to lay before Lord Aberdeen the claims of our Society to share in the accommodation thus to be provided. In December 1856 the Royal Society, at the request of the Government, allotted accommodation in old Burlington House to itself, the Linnean Society, and the Chemical Society; and in February 1857 our Society commenced to hold its meetings there. The accommodation allotted to our Society was (to quote our Minutes) as follows:—

‘The Attic Story.

‘The Ball Room and room adjoining on the North side of the building.

‘The two front rooms on the ground floor in the east end of the building.

‘The Wine-Cellar in the Basement for a Coal-cellar.’

The Ball Room, on the first floor, became the Society's library, and later, till recent years, the library of the Royal Academy of Arts. The Linnean Collections and Library, newly enclosed in handsome mahogany fittings, were placed at the north end of this room, where the outlook was on to the gardens (now covered by the exhibition galleries and the Civil Service Commission building); the adjoining room

became the Society's meeting room ; one of the rooms on the ground floor became the Council room, and the other was called 'The Herbarium Room.' In 1866 old Burlington House, with about one-half of the gardens, was made over to the Royal Academy of Arts (at that time accommodated in what is now the National Gallery, Trafalgar Square), but possession could not be taken until the new buildings (commenced in 1868 and completed in 1873) around the courtyard of Burlington House were ready for the scientific societies. Thus, for sixteen years (1857-73) old Burlington House was the home of our Society jointly with the Royal and Chemical Societies.

Old Burlington House, Piccadilly *, was built about the year 1664 by Sir John Denham, surveyor of the works to Charles II, for Richard Boyle, 1st Earl of Burlington and 2nd Earl of Cork, who was the brother of the Hon. Robert Boyle, philosopher and chemist. Previous to that date the site had been occupied by a farm house. Denham's building was a plain one of red brick ; no doubt Kip's engraving (from Knyff's drawing) of about 1700 (Pl. 1. fig. 5) gives a good idea of it. It was mentioned twice by Pepys :—[Feb. 20, 1664] 'Next that [Lord Clarendon's] is my Lord Barkeley beginning another on one side and Sir J. Denham on the other' [Sept. 28, 1668] 'Thence to my Lord Burlington's house, the first time I ever was there, it being built by Sir John Denham next to Clarendon House.' Richard Boyle, the 3rd Earl of Burlington, noted as a patron of the arts and an amateur architect, had a new south front made in 1717 by encasing the original walls with stone and raising the Venetian windows on the first floor ; and added the Colonnade in 1718. It is interesting to note that externally there was but little further change in the building until the year 1866, when contemporary photographs (Pl. 1. figs. 6 & 7) show the front of the building to be the same as it appeared in several Eighteenth Century engravings, the only difference being in the position of the chimney stacks, due to internal alterations. The Colonnade stood opposite the house (part of its shadow is seen in the foreground of fig. 6), and about one half of it occupied the ground now covered by our present quarters. This Colonnade, shut off from Piccadilly by a lofty wall, was considered one of the finest pieces of architecture in London, and aroused the enthusiasm of Horace Walpole, Sir William Chambers, and others. It is supposed to have been inspired by Bernini's great doric colonnade at St. Peter's, Rome. Upon its demolition in 1866 to make room for the foundations of the

* One of the earliest allusions to Piccadilly is in the second edition of Gerard's Herbal, 1633, where Thomas Johnson writes : 'The small wild buglosse grows upon the drie ditch banks about Pickadilla.'

new buildings, each stone was numbered with a view to its re-erection in Battersea Park, but the project was never carried out. (The stones are believed to be still in existence.) By 1873 the architect to the Royal Academy of Arts had added a superstructure (now the Diploma and Gibson Galleries) to Old Burlington House to bring the building to about the same height as the new buildings around the courtyard, and the present arcaded entrance to the Royal Academy was completed. In the same year our Society removed its belongings from Old Burlington House, leaving rooms full of the dignity of the eighteenth century for the new accommodation provided.

Burlington House, Piccadilly. With the present year the Society has occupied for sixty years the south-west portion of the courtyard buildings completed in 1873. This portion consists of a basement, ground and first and second floors, and is clearly seen as all that part of the building to the left of the archway (Pl. 1. fig. 8). Although the accommodation for the various societies was specially considered when the present buildings were designed, our own Society has of recent years felt the need of more space for its ever-growing library. One cannot but regret that, by the building of the Burlington Arcade in 1819 on a strip of ground belonging to the estate, there is now no possibility of extending westward.

EXPLANATION OF PLATE 1.

- Fig. 1. No. 12 Great Marlborough Street. (Photograph taken in 1932.)
- Fig. 2. Panton Square. (From a water colour by T. H. Shepherd in the Crace Collection.)
- Fig. 3. No. 9 Gerrard Street, Soho. (Photograph taken in 1932.)
- Fig. 4. No. 32 Soho Square. (Photograph taken in 1932.)
- Fig. 5. Old Burlington House. (Kip's engraving, c. 1700.)
- Fig. 6. Old Burlington House. (Photograph c. 1866, reproduced by courtesy of the Editor of 'Country Life'.)
- Fig. 7. The Colonnade, Old Burlington House. (Photograph, c. 1866, reproduced by courtesy of the Editor of 'Country Life'.)
- Fig. 8. South front of Burlington House, Piccadilly. (Photograph taken in 1932.)

Lt.-Col. A. T. GAGE added some comments, including a reference to the origin of the name 'Burlington', which was derived from Bridlington in Yorkshire, the Earldom of Burlington (or Bridlington) having been granted to Richard Boyle, the 2nd Earl of Cork.

The swimming movements of *Diaptomus gracilis* revealed by use of the Cine film. By Mr. A. G. Lowndes.

OWING to the shortage of time Mr. Lowndes was unable to go beyond an account of the construction and method of working of his polygraphic apparatus.

The Viability of Seeds. By Mr. J. H. Turner.

THE problem of seed viability has long proved of interest to botanists and those engaged in any form of agriculture.

Theophrastus mentions that 'of seeds some have more vitality than others as to keeping', but little was known about the vitality of seeds of wild plants until De Candolle, in 1832, concluded that the seeds of many species remained viable in the soil for considerable periods.

Since De Candolle's time much has been written regarding this subject, but the literature is very scattered, and with few exceptions the accounts are based upon observations rather than experiments.

Only a limited number of cultivated plants produce seeds which retain their vitality for any length of time when buried in the soil, but those of 'weeds' are capable of living for extended periods, and when deeply buried are better preserved as a result of the more equable conditions.

A. W. Hill, in an account of the flora of the Somme battle-field, describes the amazing growth of poppies, chamomile, and charlock, *Brassica Sinapistrum* Boiss., from latent seeds brought to the surface by shell-fire; and the appearance of charlock on earth thrown up by shells and in shell-craters, when there was no trace of it on the undisturbed ground, was remarked by other botanists during the War.

Peter showed that seeds of charlock can retain their vitality in the soil for forty years, whilst Dorph-Petersen found that, although the germination of stored seeds of charlock after ten years was only 24 per cent., those buried for the same period gave a germination of 87 per cent.

E. J. Salisbury relates that during the building of a house on former arable land, corn-field weeds appeared, and notably plants of *Anagallis foemina* Mill., a species rare in that locality. The ground had been under hay for more than sixty years, and was no doubt laid down to grass at the end of the Napoleonic wars.

A similar occurrence of *Fumaria officinalis* Linn. is described by H. W. Pugsley.

There are many instances of the longevity of buried leguminous seeds, and the appearance of plants of *Ulex europaeus* Linn. after the seeds had been buried for forty, twenty-five, and twenty years is recorded by Trochu, Parkin, and J. C. Shenstone.

Pugsley describes the growth of *Cytisus scoparius* Link on the bare slopes of a road cut through land that nearly a century ago bore this plant, whilst Ewart, in Australia, found seeds of *Acacia* spp. buried deeply in *Eucalyptus* forests,

where there were no other acacias within a mile; he also found under trees of *Acacia dealbata* Link seeds buried eighteen inches below the ground which gave perfect germination.

A. Pratt, and recently A. B. Jackson, record the appearance of *Digitalis* on disturbed soil, and it would seem that the seeds must have retained their vitality for several years.

O'Brien found that when land previously under grass for forty years was disturbed *Verbascum* came up in quantity.

According to Comber, it is evident that seeds of *Onopordon* may remain viable for twenty-five years.

W. E. Brenchley found that when grassland which had replaced arable was turned up typical arable weeds grew from seeds which had lain dormant in the soil for periods up to 58 years.

Probably the record longevity for any seed is that obtained by Ohga, who germinated approximately 100 per cent. of the 'seeds' of *Nelumbo nucifera* Gaertn. found on a peat bed under two feet of loess in Southern Manchuria. It is probable that the 'seeds' are at least 120 and may be 400 years old. Ohga gave thirty of these 'seeds' to the British Museum, and in 1931, at the request of Sir Arthur Hill, the British Museum authorities sent two of these 'seeds', which they had germinated, to Kew. The seedlings were planted in the *Victoria regia* pool and flowered during August 1932. Apart from the smaller flowers and seed vessels there was nothing to distinguish them from plants raised from recent 'seeds'.

The only satisfactory methods of ascertaining the length of time that buried seeds will remain viable are by experiments such as those begun by Béal and Duvel in the United States. In 1879 Beal mixed seeds with sand and buried them in bottles. The results of this experiment show that after fifty years seeds of *Brassica*, *Oenothera*, *Polygonum*, *Rumex*, and *Verbascum* still germinate.

Duvel experimented under more natural conditions and found that, of 107 species, 51 grew after being buried for twenty years.

Not only seeds buried in the earth, but those submerged in mud and water, have the power of resting until conditions favour germination. This has been demonstrated by Darwin, Salter, White, Guppy, Shull, Salisbury, and others. There are numerous instances of the germination of stored seeds. In 1850 Robert Brown experimented with 'seeds' of *Nelumbo* from the collection of Sir Hans Sloane (in the British Museum) and found that 88 per cent. of the fruits had retained their power of germination for about 150 years.

Bequerel tested seeds of known age from 25 to 135 years in the Herbarium of the Natural History Museum of Paris. The oldest seed found viable was *Cassia bicapsularis* Linn.—after 87 years.

The writer experimented with seeds collected by Dr. Bromfield in the Isle of Wight in 1842, and also with seeds sent to Kew in 1851 by Peter Lawson & Co. These are preserved in loosely corked bottles in the Museums. The following seeds of Leguminosae germinated after treatment with concentrated sulphuric acid :—

	Years.	
<i>Anthyllis Vulneraria</i> Linn.....	90	4 per cent.
<i>Trifolium striatum</i> Linn.	90	14.1 per cent.
<i>Trifolium pratense</i> Linn.	81	2.6 per cent.
<i>Lotus uliginosus</i> Schkuhr.	81	9.6 per cent.
<i>Melilotus alba</i> Desv.	81	163 seeds, 1 germinated.
<i>Cytisus scoparius</i> Link.	81	636 seeds, 4 germinated.
* <i>Medicago orbicularis</i> All. ... at least	78	22 per cent.
Also <i>Ipomoea</i> sp.	43	6 per cent.

The seedlings are now growing in one of the houses at Kew. Seeds of Polygonaceae, Cruciferae, Papaveraceae, and Scrophulariaceae failed to germinate.

Ewart formed the opinion that seeds cannot indefinitely prolong their vitality, and that the probable extreme duration of vitality for any known seed may be set between 150 and 250 years.

Some of the instances of supposed seed viability are unsupported by definite evidence, and the 'classical case of seed longevity' described by Heldreich was evidently founded on taxonomic errors. Heldreich puts forward the suggestion that the sudden appearance in the Laurion area (Greece) of *Silene juvenalis* Delile, and a supposed new species which he named *Glaucium Serpieri* Heldr., was due to their seeds having remained dormant for more than 1500 years in the soil under the heaps of old mining débris. A taxonomic investigation made by Turrill has shown that *Silene juvenalis* is conspecific with *S. subconica*, a not uncommon species in the countries around the Aegean Sea. There is nothing in the taxonomy or distribution of *S. subconica* and *Glaucium Serpieri*, which has been shown by Turrill to be *G. flavum* var. *leiocarpum* Stoy. & Stef., to make it improbable for them

* The seeds of *Medicago orbicularis* All. formed part of a carpological collection given to George Bentham, who, on June 29th, 1854, presented them to the museum of the Royal Botanic Gardens.

to occur naturally in the Laurion district, and in all probability both species were in the neighbourhood before the heaps of débris were removed, and simply spread on the vacated and denuded ground in the absence of close competition.

Cereals are ill adapted for a prolonged period of quiescence, and there is no authenticated evidence that wheat taken from undisturbed Egyptian tombs will germinate. It is popularly asserted that 'Miracle' wheat, *Triticum turgidum* var. *mirabile* Körn. and 'Mummy' peas, *Pisum sativum* var. *umbellatum* (Mill.) Ser. originate from Egyptian tombs and that such seeds germinate when sown, but in every instance the statements prove to be without foundation.

Sir SIDNEY HARMER referred to the occasional occurrence, in large numbers, of *Epilobium angustifolium*—of which he had seen a notable example in an unoccupied area in the Strand, some years ago. He enquired whether there was evidence indicating that this should be regarded as an instance of the kind described in Mr. Turner's paper or was more probably the result of wind-borne seeds.

Mr. T. A. DYMES and Mr. I. H. BURKILL referred to similar appearances of *Epilobium angustifolium*, and agreed that the characteristic seeds would indicate that wind distribution could account for this well-known phenomenon.

Mr. J. RAMSBOTTOM pointed out that Robert Brown's experiments with 'seeds' of *Nelumbium* were in four series and extended over a period of twelve years. The seedlings were at present on exhibit in the Gallery at South Kensington, together with the 'seeds' deposited in the British Museum by Professor Ohga.

Four zoological exhibits. By Captain J. G. Dollman.

1. Captain Dollman exhibited the head of a Capuchin Monkey (*Cebus apella*) recently collected in the island of Trinidad, and sent to the British Museum (Natural History) by Professor Ballou, of the Imperial College of Tropical Agriculture, Trinidad. He remarked that it was the first time that this monkey had been recorded from Trinidad, the species having previously been known only from the Guianas, the type-locality being Dutch Guiana. It was quite possible that this monkey spreads northwards into Venezuela, from whence its passage into Trinidad would present no great difficulty. From the condition of the skull it was obvious that the specimen was a wild-killed one and not a menagerie example.

Attention was drawn to the only other monkey known from the island, a species of Howling Monkey, *Alouatta*

insulanus, described by the late Professor Elliot as distinct from the mainland form, *Alouatta senicula*.

2. A Plague of Desert Gerbils (*Cheliones hurrianæ*) in Bikaner formed the subject of a second exhibit, Captain Dollman stating that he had received a communication from Mr. F. K. Jackson, agricultural adviser to the Central Indian States and Rajputana, concerning a plague of gerbils then raging in Bikaner. Mr. Jackson reported that considerable damage had been done to the cotton-crops by these pests, and he sent home some specimens of the gerbil for identification. These proved to be specimens of the Indian desert gerbil (*Cheliones hurrianæ*) originally described by Jerdon in 1867 as *Gerbillus hurrianæ*. Captain Dollman read a report from one of the agricultural officers of Bikaner in which the overwhelming nature of the plague was fully set forth, and remarked that the gerbils were evidently present in very vast numbers, since the fields were honeycombed by their burrows, and the situation might be regarded as a very serious one, the animals always being excessively numerous, but in certain years overwhelmingly so.

3. The skin and skull of a hybrid between a lion and a leopard, recently presented to the Museum by Colonel F. W. Wodehouse, C.I.E., was also exhibited. This hybrid, which was bred in the Gardens of Kolhapur, resulted from a union between a male leopard and a lioness, and lived to be about three years old. At first sight the skin resembles that of a leopard, but the spots are much browner and less distinct than those of the typical Indian leopard, the tail is slightly tufted, and the underparts a dirty white rather than the pure white of the leopard. The skull, which has been examined by Mr. R. I. Pocock, F.R.S., appeared to be more leonine than pardine in character, except that the upper carnassial tooth was more like that of a leopard than that of an Indian lion.

In the discussion that followed the President made some humorous remarks concerning the name of 'Leon' which had been proposed by Captain Dollman for this hybrid, and suggested that the name might be written 'Lepon'. Another suggestion was forthcoming that the name should be 'Pardon'. In spite of this latter very pardonable title Dr. Calman registered his regret at such gross interference with the English language, and gave the Meeting to understand that he had not wholly recovered from the shock received at the first hearing of the name of 'Tigon'.

4. Two models of albino elephants were also exhibited by Captain Dollman. One of these models represented a typical Siamese elephant, made to the order of Major Stanley Flower by a Siamese modeller, and passed by the Siamese elephant-

men as being a perfect representation of an albino elephant. The other model, the work of Mr. F. T. Daws, was of the Burmese white elephant which was on loan to the Zoological Gardens of London some years ago. Captain Dollman drew attention to the fact that there was no record of a white elephant from Africa, and remarked that, in view of the vast numbers of elephants shot and observed in that Continent during the last hundred years, this was a surprising state of affairs.

Dr. W. T. CALMAN, in the discussion that followed, stated that, although he realized such models were of value to the student, he deprecated their exhibition to the public, on the ground that they attracted attention away from the natural and normal to the exceptional and abnormal.

19 JANUARY 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 5 January 1933, having been circulated, were taken as read and confirmed.

The PRESIDENT reported the death of Basil Harrington Soulsby, Fellow of the Society, and referred to his bibliographical work in its relation to Linnaeus.

The PRESIDENT announced that the General Meeting on 16 February next would be devoted to the Hooker Lecture, which will be delivered by Professor Sir William Wright Smith.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—Irene Alexandra Francis Hilton and Harold Alexander Wootton.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Leslie John Walker ; for the first time, in favour of Lawrence Root Waldron.

The following candidates were balloted for and elected as Fellows :—Professor Frère Marie-Victorin, D.Sc., Rubugunde Madhava Row, B.A., Norah Lillian Penston, Ph.D., and Robert Henry Corstorphine, B.Sc.

Contributions to our knowledge of the Colonial Volvocales of South India. By Professor M. O. P. Iyengar.

IN giving an account of Prof. Iyengar's communication Prof. F. E. FRITSCH pointed out that it dealt with a large number of different forms and contained numerous valuable observations. It was only possible to draw attention to a few of the more striking types. As a result of Iyengar's studies *Eudorina illinoiensis* (Kofoid) Pascher (*Pleodorina illinoiensis* Kofoid) was given greater precision, since according to him the essential characteristic of the species lies in the fact that the four anterior cells of the coenobium always behave differently from the others ; often, for instance, they remain vegetative, while the other cells produce daughter-colonies, or, in monoecious coenobia, they form antheridia, while the remaining cells become ova. A new species of *Eudorina* with 64-celled colonies shows two transverse tiers of smaller cells at the anterior pole, those of the second tier being somewhat larger than those of the first. Of particular interest is a new species of *Pleodorina*, where the gonidial cells are scattered among vegetative cells in the posterior part of the colony, gonidial cells being absent only from the anterior fifth. This form shows an approximation to the condition found in *Volvox*, where, however, the proportion of gonidia to vegetative cells is far smaller. Prof. Iyengar's paper also deals with a considerable number of forms of *Volvox*, several being species well known from Africa, but hitherto not known to occur in India. A new species is characterized by the successive formation of reproductive cells throughout the life of the colony.

Observations on Volvox in Africa. By Miss F. Rich.

VERY little was known concerning the occurrence of the genus *Volvox* in Africa until four or five years ago. Dr. M. A. Pocock then had the opportunity of collecting and examining it from several places, notably from Vleis or Pans on the Cape Flats, and in cultures from Rietfontein in the Transvaal. The *Volvox* from the former locality is regarded as a new species ; the other is identified as *V. Rousseletii* G. S. West. From studies on living, or freshly killed, material Dr. Pocock has succeeded in following all stages in the inversion of the young daughter-colonies, and has proved for the first time

that this curious process also goes on in the developing sperm-bundles and in the colony formed by the germinating oospore. The oospore may begin to germinate almost immediately on liberation, or it may rest for years. Direct sunlight is necessary for germination, while complete drying-up, though not essential, is beneficial. *V. Rousseletii* has been proved to form a motile zoospore; previous writers have expressly stated that in the species of *Volvox* examined by them no such zoospores were produced. Dr. Pocock has also shown that the colonies formed from the germinating oospores are considerably smaller than the later colonies, and are composed of fewer cells. These 'juvenile colonies' are so remarkable that, when first seen, they were mistaken for a new genus. It is only in the third generation that true adult colonies appear.

It has been established that *Volvox* is very widely and abundantly distributed in Africa.

In a discussion on the two preceding papers, Prof. F. E. FRITSCH commented on the careful work of Miss Pocock on the two African forms of *Volvox*, and especially on the discovery of the mode of development of the zygote. A very considerable contribution to our knowledge of this genus in Africa had been made by Miss Rich and Miss Pocock. At the same time he felt some doubts as to the specific status of most of the African forms of *Volvox*, excepting *V. africanus*. The differences from the European forms were in great part only differences of degree, and might well be related to the wide geographical range involved.

Professor R. R. GATES asked whether the various genera into which the genus *Volvox* had been subdivided by Shaw were recognized as distinct. He referred to the work of Akehurst on *Eudorina*, in which trumpet-shaped structures, each containing a pair of cilia, were described in the wall of the colony, and asked whether similar observations had been made in any other forms. He also asked why *Pleodorina illinoiensis* was transferred to the genus *Eudorina* and yet *P. californiensis* was retained and a new species of *Pleodorina* added to it.

In reply to Prof. Gates, Prof. FRITSCH said that it was scarcely possible to go into Shaw's genera in the available time, but he drew attention to the fact that they had not been accepted by any recent authority.

Mr. A. J. WILMOTT gave an account of the following paper:—

On the synonymy of *Cornucopiae alopecuroides* L.

By A. Elg, Hebrew University, Jerusalem.

IN Journ. Linn. Soc. xxiv (1888), p. 440, the Rev. Dr. Post published a new species of *Alopecurus*, *A. involucratus*, from

Syria. In 1921, C. Mez (in Fedde Rep. xvii, p. 293) changed the generic name of this plant, assigning it to *Cornucopiae*, *C. involucreatum* (Post) Mez, without any explanation or notes, and in 1927 * I discussed this question and came to the same conclusion. In the present article I wish to try to show that the true name of the plant is *Cornucopiae alopecuroides* L., thus removing an injustice to one of the Linnean plant-names, an injustice caused principally by an article which appeared in the 'Transactions of the Linnean Society' more than 125 years ago.

Cornucopiae was already mentioned by Scheuchzer †, who also gives the first drawings of a species of this genus (tab. iii, fig. 1, a, b, c, d). The description and the drawings are sufficiently clear to enable recognition of *Cornucopiae cucullatum*; Scheuchzer probably did not know the second species of this genus.

The works of Linné up till 1757 mention only one species of the genus *Cornucopiae*, *C. cucullatum*, and only in the 'Mantissa' of 1767 ‡ do we find the description of the second species of *Cornucopiae*, *C. alopecuroides*, as follows:—

'*Cornucopiae alopecuroides*: Habitat in Italia. Arduini. Spica aristata cucullis hemispherica recepta. Simillium Gr. Alopecuro pratensi culmi adscendentes, laeves. Folia laevia. Spica terminalis, ovata, laxa, flosculis brevissime pedicellatis. Calycis gluma bivalvis, aequalis, ovata, acuta. Corollae gluma univalvis, longitudine calycis, cui opposita est; arista patens flore duplo longior, vagina supremi folii ventricosa ut in Phalaride. Singularis nota est urceolus hemisphaericus, integerrimus, consistentia folii, qui instar calycis communis cingit basin spicae.'

It is true that some of the details of this description do not apply exactly to our *C. alopecuroides* from Syria and Palestine, but the drawing of Arduini's plant represented in the Trans. Linn. Soc. in 1804 by J. E. Smith leaves no doubt that *C. alopecuroides* from Syria and Palestine and the plant which Linné received from Arduini belong to one and the same species. (Compare the two drawings.)

How is the complete disappearance of *C. alopecuroides* L. from modern botanical literature to be explained? In J. E. Smith's article entitled: 'An Illustration of the Grass called by Linneus *Cornucopiae alopecuroides*' (Trans. Linn. Soc. vii, 245–248 (1804), tab. xii, fig. 1), he tries to prove that *C. alopecuroides* does not belong to the genus *Cornucopiae*,

* A. Eig, 'A Second Contribution to the Knowledge of the Flora of Palestine.'

† Scheuchzer, 'Agrostographia,' 1719, p. 117.

‡ Carl von Linné, 'Mantissa Plantarum Generum ed. vi et Specierum ed. ii,' p. 29.

and that it may be a variety or a monstrosity of *Alopecurus utriculatus*. He adds that Sir Joseph Banks also examined this plant of Linné and arrived at the same conclusion.

Some years later (1812), Palisot de Beauvois ('Agrostographia,' pp. 4-5) also reports the two species of *Cornucopiae*,



1. A copy of a drawing of the original Linneus *Cornucopiae alopecuroides* by J. E. Smith on tab. xii, fig. 1, in vol. vii (1804) of Trans. of the Linn. Soc.
2. Drawing of a Palestine specimen from the Herbarium of the Hebrew University of Jerusalem.

C. cucullatum and *C. alopecuroides* (pl. i, fig. 7, and pl. iv, fig. 4, a, b, c, d). These drawings correspond to those of Smith's original plant of Linné and to our plants of Syria and Palestine, despite the very small heads and the absence of blades on the upper leaf.

Nevertheless, Roemer and Schultes (Syst. Veget. (1817), ii, p. 252) added below the description of *Cornucopiae cucullatum*:—‘*Cornucopiae alopecuroides spica aristata* Linn. Mant. p. 29; Syst. Veget. p. 103; Willd. Spec. 1, p. 319; Vahl Enum. ii, p. 393 *varietatem esse mal assernotam Phalaris utriculatae* (qua valis *Alopecurus*) *annulo nompe cartilagineo ad basin apicae dilatate in formam involucri cyanthiformis, ut in genere Cornucopiae*, J. E. Smith in Linn. Trans. vii, p. 245; Sibth. Fl. Gr. 1, p. 43.’

Thus Roemer and Schultes accepted the opinion of Smith as opposed to that of Linné and Palisot de Beauvois. All the later botanists whose works I was able to consult followed them. Thus *Cornucopiae involucreatum* L. disappears from the later botanical literature*. As no one was able to find this plant either in Italy, where Linné supposed it to be growing, nor in any other country where *Alopecurus utriculatus* grows, it ceased to be mentioned in botanical literature also as a variety of *A. utriculatus*.

When in Europe I endeavoured to find traces of this species in the different herbaria which I visited. At Dahlem, Berlin, I found no plant named *Cornucopiae alopecuroides*, although in the packet of *Alopecurus utriculatus* I found one specimen of this species from Palestine. At the Conservatory in Geneva I saw several specimens of *C. alopecuroides*, all collected in Syria and Palestine; some of them well determined by the old authors. But the only place where I found this plant under the name of *C. alopecuroides* in a special packet was the Herbarium of the Principal Botanical Garden in Leningrad. Under this name there are two specimens, both from Syria. Thus all the specimens I have seen in the different herbaria originated from Syria or Palestine, countries where it appears to be endemic. How the Italian origin of the specimen of Linné may be explained, I cannot say. Possibly Arduini's plant was an adventive one.

In Palestine this species is rather common in places inundated in winter, or in habitats wet all the year round, in the maritime plain and in Galilee. In Syria, too, we found it only in the same habitats.

Hence the synonymy of *Cornucopiae alopecuroides* L. is: *Alopecurus utriculatus* var. *alopecuroides* J. E. Smith = *Alopecurus involucreatus* Post = *Cornucopiae involucreatum* (Post) Mez.

The variety which I described in 1927 under the name of *Cornucopiae involucreatum* var. *heteraristata* must be named *C. alopecuroides* var. *heteraristata*.

* See, for example, Engler und Prantl, ‘Die Pflanzenfamilien’; ‘Kew Index’; Boissier, ‘Flora Orientalis,’ etc.

Mr. WILMOTT added the following 'Note on the *Crypsis alopecuroides* in Herb. Linn.':—

I have examined the specimen in the herbarium. The sheet is labelled '*alopecuroides*' in Linnaeus's hand, and bears a note by Sir J. E. Smith—'*certe Phalaris utriculata*.' The specimen is certainly not *Alopecurus utriculatus*, and is as certainly *Cornucopiae involucratus* (Post) Mez. The specimen is marked by Linnaeus on the sheet as from 'Ard.', and the sheet bears a ticket by Arduino—'Nr 82', with a rough sketch of the inflorescence pointing out the characteristic 'urceolus'.

The specimen has the upper margin of the urceole undulated as in the wild specimen figured by Dr. Eig, and not straight as figured by Smith.

In the Linnean correspondence are letters from Arduino containing lists of the numbered specimens sent to Linnaeus with Arduino's identifications. The longest of these reaches only to a Nr 76 (ending with several grasses), but the letter with it indicates that Arduino's bundle contained some plants about which he is uncertain, others which Linnaeus may not possess, and others which he cannot identify. Presumably this Nr 82 was one of these last. But there is nothing in the letter warranting an assumption that the specimens were Italian. Certainly Linnaeus discussed other than Italian plants with Arduino, for in a letter to him printed in the 'Proceedings' of this Society (1907, p. 86) he writes:—'*Astragalus chinensis* mihi duplex est: tuus erit sine dubio parvus acaulis purpureus quem habeo . . .'

As Linnaeus was by no means impeccable concerning the habitats he gave for his species, it may reasonably be presumed that in this case the 'Italia' is merely an erroneous assumption, and is no objection to the views expressed in Dr. Eig's paper.

A comparative study of geotropism in three species of *Lupinus*. By Miss E. D. Brain.

THE course of graviperception as measured by the Presentation Time has been traced throughout the life-cycle of *Lupinus albus*, *L. polyphyllus*, and *L. arboreus*. Ontogeny of graviperception has been studied in detail in the seedling of *L. albus* and inflorescences of *L. albus* and *L. arboreus*. Specific differences of behaviour are marked in the inflorescence stages of the plant, and it is suggested that these may be correlated with specific differences of life-habit.

The PRESIDENT, in thanking the speaker, asked whether she had examined the statolith apparatus in the *Lupin* seedlings.

Miss T. L. PRANKERD said that Miss L. Hawker (Ann. Bot. 1932) had shown the close correspondence between the curve for the amount of statolith time and that for graviperception in several seedlings. Further, Miss Brain's work was a warning to physiologists against assuming the general validity of quantitative work on a single species.

In reply, Miss BRAIN said that Haberlandt demonstrated statoliths in the tips and growing region of *L. albus* radicles. She herself had not made microscopical examinations, but Miss Hawker had shown complete correlation between the distribution of the statocyte tissue and the response to gravity in the hypocotyl.

2 FEBRUARY 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 19 January 1933, having been circulated, were taken as read and confirmed.

The President announced the death of Lt.-Col. John Stephenson on the 2nd February 1933, and moved the following Resolution, which was passed in silence, all standing :—

The Linnean Society of London having heard with the deepest sorrow of the death of Lt.-Col. John Stephenson, C.I.E., F.R.S., Zoological Secretary of the Society, desire to record their gratitude for the great services which he rendered to the Society and their sympathy with Mrs. Stephenson.

The President also announced that Dr. W. T. Calman, F.R.S., had kindly consented to deal with any urgent matters requiring the attention of the Zoological Secretary, pending a new appointment.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—Robert Henry Corstorphine, Norah Lillian Penston, and Rubugunde Madhava Row.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Lawrence Root Waldron ; for the first time, in favour of Bindiganavale Thirumalachar and Thengumparampil Kurien Koshy.

The Cichlid Fishes of Africa.

By Miss Ethelwynn Trewavas.

THE Cichlidae are a family of Perciform fishes that inhabit the fresh waters of South and Central America, of Africa, and Madagascar, with a genus in India and Ceylon. They are fairly generalized perches, but are distinguished by the presence of a single nostril on each side, by having only sixteen principal rays in the caudal fin, by the absence of a subocular shelf, by the toothless palate, and the sutural union of the lower pharyngeal bones.

For breeding they pair, and the eggs and young are sheltered in the mouth of one of the parents.

Division into genera was at first very artificial, for the characters used, chiefly of dentition, although sometimes reliable, are often very different in closely related species, or may even change with age.

Dr. Tate Regan's studies on the African genera, beginning in 1920, showed that the structure of the apophysis on the base of the skull for the attachment of the upper pharyngeal bones is of two types, and that by means of it the genera may be grouped in two main divisions. *Tilapia* and related forms have the pharyngeal apophysis formed by the parasphenoid alone. *Haplochromis* is the largest genus in which the basi-occipital also takes part in the formation of the apophysis.

Further division of the main groups into genera is very difficult, owing to the great evolutionary vigour of the group. In the African great lakes the Cichlidae appear to have found ideal conditions, and have evolved into numerous closely related species, which fill every possible ecological niche in the lakes, availing themselves of every type of food-material present, and showing modifications in form and dentition which may often be correlated with the feeding-habits. Dr. Tate Regan's revision of the Cichlidae of Lake Tanganyika * recognized 89 species of 37 genera in this lake. In Lake Nyassa † there are fewer genera, but many more species, mostly of *Haplochromis* and related genera. Several striking instances of parallel evolution are provided by the Cichlids of Lakes Nyassa and Tanganyika, and other Nyassa and

* Regan, C. Tate, 1920. 'The Classification of the Fishes of the Family Cichlidae.—I. The Tanganyika Genera.' *Ann. & Mag. Nat. Hist.* (9) v, pp. 33–53.

† Regan, C. Tate, 1921. 'The Cichlid Fishes of Lake Nyassa.' *Proc. Zool. Soc. London*, 1921, pp. 675–727, 30 text-figs, 6 pls.

Tanganyika species find parallels also in the Victoria Nyanza. Here the species of *Haplochromis* are numerous and diverse, but generic divisions are not well marked*.

The Lake Edward fish-fauna is mainly Cichlid, and Dr. Worthington's collection enables us to recognize six species in common with Lake Victoria, seventeen endemic and two Nilotic species. One of the latter is the widespread *Tilapia nilotica* (already recorded from the lake); the other, *Haplochromis multicolor*, was found in the Semliki River, not in the lake itself. The endemic *Haplochromis* are all closely related to Lake Victoria species. The endemic *Tilapia* represents the two Lake Victoria species†, with some of the characters of each. *Schubotzia*, the endemic genus, was not represented in this collection.

Lake Rudolf resembles Lake Albert in having a Nilotic fish-fauna, mainly non-Cichlid. The Cichlidae comprise three species of *Tilapia* common in the Nile, a new endemic species of *Haplochromis*, and a new species of *Pelmatochromis*. The presence of a *Pelmatochromis* is very surprising, since the genus is a West African one, not represented in the Nile.

As Dr. Regan wrote in 1922, 'If the degree of differentiation be taken as a guide, one may form the conclusion that the Cichlidae have inhabited Tanganyika longer than Nyassa, Nyassa longer than Victoria.'

The new collections abundantly confirm the earlier suggestion that the present fish-fauna of Lake Edward is derived from the Victoria Nyanza, with very little connection with Lake Albert and the Nile, and that Lake Rudolf was formerly connected with the Nile system. In addition, a hint is given of a more ancient connection between Lake Rudolf and the West African drainage-system.

Dr. C. TATE REGAN said that he and Miss Trewavas were collaborating in an attempt to put the Cichlidae in order. This was a large family, including probably a thousand species, and it was very difficult to classify, unless one were content to have one or two very large genera that included a great diversity of species, and to separate from these a number of small, mostly monotypic, genera, each distinguished by some specialized feature.

Mr. J. T. CUNNINGHAM said that he had been especially interested in the adaptive modifications related to different kinds of food and methods of feeding described by Miss Trewavas, and in the fact that such modifications were quite independent of specific characters and relations.

* Regan, C. Tate, 1922. 'The Cichlid Fishes of Lake Victoria.' Proc. Zool. Soc. London, 1922, pp. 157-191, 14 text-figs, 4 pls.

† See Graham, M., 1928. Ann. & Mag. Nat. Hist. (10) ii, pp. 209-13, pls. ix-xi.

Two zoological exhibits. By Captain J. Guy Dollman.

Captain GUY DOLLMAN exhibited a skull of a man-eating Lion, recently presented to the Museum by Mr. Keppel-Compton, who obtained the specimen in Marimba, Nyasaland, in February 1926.

This lion was responsible for deaths of between forty and fifty natives from villages near the junction of the Bua and the Ruca rivers in Marimba. The animal was eventually killed in a single-handed encounter by a native, who hid behind a tree within close range of the half-eaten body of his brother and when the man-eater returned to the kill, courageously attacked the beast with his spear, and then finished it off with an axe. The interesting part about the skull is that the canine teeth are worn down or broken, and the left side of the skull, in the region of the zygomatic arch and mandible, shows signs of extensive injury during the animal's existence. Thus the jaws of this beast, were perhaps, partially paralysed and this may have led to it preying upon man as being more easily killed than its natural ungulate victims.

A second exhibit dealt with the various species of Rhinoceros now existing, with special reference to a recent report regarding the occurrence of the Javan Rhinoceros (*Rhinoceros sondaicus*) in Sumatra. It was, he pointed out, now definitely proved that this species was indigenous to the island of Sumatra, and the original type-locality, as given by Desmarest in 1822, was undoubtedly correct. The fact that Desmarest had given Sumatra as the locality for his *sondaicus* had long been regarded with suspicion, a suspicion that now proves ill-founded.

Lantern-slides were exhibited of various types of Rhinoceros, including a slide made from a photograph of a *Rhinoceros sondaicus* which had been shot in Sumatra.

Mr. H. N. RIDLEY stated that he had once come across a *Rhinoceros sondaicus* in Pahang, and that its scarcity was doubtless due to the value attached to the horn, causing it to be hunted down. When attacked it did not use its horn for defence, but bit pieces off its assailant, and the late Dr. Lotsy had told him he had seen a beater in Java bitten in two by one. The commoner *R. sumatrensis* in the Malay Peninsula always has black hair, not red as is described from Burmah.

The rust of wheat and barberry. By Mr. J. Ramsbottom, O.B.E., Sec.L.S.

ONE of the beliefs which gained credence with farmers and others in the latter part of the eighteenth century was that barberry bushes somehow affected wheat, disposing it to blight.

The well-known Province Law of Massachusetts, 1755, entitled 'An Act to prevent damage to English grain arising from Barberry bushes', begins, 'Whereas it has been found by experience, that the blasting of wheat and other English grain is often occasioned by barberry bushes, to the great loss and damage of the inhabitants of this province.' Similar laws for the removal of barberry plants apparently were passed at Connecticut and Rhode Island and at Rouen. Marshall, in the *Rural Economy of Norfolk* (1787), writes that 'It has long been considered as one of the first vulgar errors among husbandmen that barberry has a pernicious quality (or rather a mysterious power) of blighting wheat which grows near it', and gives facts which go to support the belief. For many years there were heated discussions about this matter, what Lind has called 'the Barberry war', and has likened to a second Thirty Years' War.

Arthur Young, then Secretary to the Board of Agriculture, issued a circular in 1804 with twelve questions about the occurrence of wheat mildew. One of these reads, 'Have you make any observations on the barberry, as locally affecting wheat?'. Answers to these queries were analysed and published in the 'Annals of Agriculture'; many of the facts were used in the series of General Views of the Agriculture of the English counties.

In 1805 Sir Joseph Banks published his well-known 'A short account of the cause of the disease in corn, called by farmers the blight, the mildew, and the rust'. This appeared in several journals and was also issued as a pamphlet, of which there were three editions. The eminence of the author led to a greater interest in the more scientific aspects of the problem. Thomas Andrew Knight, the famous horticulturist, apparently was consulted by Banks, for there is a copy of a letter in the Banksian correspondence, which reads :—

' Elton. Dec. 29th. 1804.

'I return you a great many Thanks for your excellent delineation of the cause of Blight, and shall be highly gratified by the further Information you promise me.'

The 'excellent delineation' is doubtless the drawings of Francis Bauer, some of which were reproduced in the pamphlet. Bauer's excellent series of drawings of 'Diseases in Corn' are in the Department of Botany. There is a letter from Knight appended to the second edition of Banks's pamphlet, and in it are described what I believe are the first experiments on heteroecism. The following extracts from the Banksian correspondence serve as a commentary on the letter, which was apparently written for publication at Banks's request :—

‘ Elton. Monday Aug. 12th. 1805.

‘ I told you in my last that I could not discover any organised Body on the Barberry similar to the Rubigo on the Wheat. I had attentively examined the leaves in young Shoots, but I had neglected the Fruit, on which, yesterday Morning, I found the Rubigo in exactly the same state as on the Corn. Brushing off some of the seeds of it from each Plant, I placed them in the Microscope; and in Colour, Form, and in every respect, they were the same, except that some of the seeds from the Corn-straw appeared, I thought, rather, if any Thing, larger than the seeds on the Barberry: but the difference was scarcely perceptible, and the Plant itself was rather more luxuriant on the Corn than on the Barberry. The Rapidity, with which the Rubigo advanced towards Maturity, greatly exceeds any Expectations, which you had, I believe, previously formed. Three days ago, on Thursday last, I observed by the aid of my Pocket compound Magnifier little Elevations on the straw of a Wheat Plant; and this morning I observed the seeds on the same Points perfectly ripe, and adhering to my Finger on Contact with it. I can not be mistaken in the Plant, because I marked it by tying a Thread round it, and have subsequently observed, twice a day, the Progress of the disease. I am perfectly satisfied now that the brown mildew on the Appletree and Blackthorn is of a perfectly distinct Species, if it be a Congener; and I am confirmed in this opinion, from the Circumstance that the Wheat in the orchards of this County is always as free from Blight as in other situations.

‘ I have endeavoured to propagate the Rubigo in various ways; and I hope to be able to give a good account of it in a few days. Its seeds seem incalculably numerous, like those of other Fungi: did I ever mention to you an attempt I made some Years ago to count the seeds of a large Mushroom in my Vinery. Of course, I cannot pretend to perfect Accuracy, but by placing Plates of Talc under it during the whole time of its seeding, and ascertaining with some degree of accuracy the Number which fell within an Hour in the small space of the Field of a powerful Magnifier, I removed all doubt from my Mind, that the Number of seeds it afforded, exceeded 500,000,000*. We may therefore easily account for the Ubiquity of Plants of this Species: and other fungi are probably not less exuberantly prolific. If I am successful in propagating the Rubigo and in ascertaining its age and progress,

* This estimate is remarkable considering the method by which it was obtained. A. H. R. Buller (1909) calculated that a fruit-body of *Psalliota campestris* with a pileus 8 cm. in diameter deposited 1,800,000,000 spores.

I will write again in a few days; and if you think the Experiments I have made on the white Mildews and the observations in their Rubigo worth communicating to the Public, I shall be happy in receiving your directions.

‘ Elton. Aug. 23rd. 1805.

‘ Respecting the Rust I am wholly at a loss what to say or think. I do not at all understand the Characters, by which the Fungus on the Wheat is made a distinct Genus from that on the Barberry. The seedvessel of the brown and white Mildews and of the Rust on Wheat are in the Microscope oblong; and that of true Rust, as I shall call it, on the Barberry is nearly round; but, as many Plants, as the Primrose, undergo great Changes from different soils, merely from their different degrees of Richness, may not the Rust of the Wheat assume a different Form when it derives its Food from the astringent acrid Berry of the Barberry Tree?. Our best Botanists appear to me to blunder very often between Species and Varieties in larger Plants; and I am very much disposed to doubt their accuracy in this Case. I confess I can not discover one great difference in the Rust on the Barberry compared with that on the Wheat; and I am therefore led to suspect that the Fungus you mention may be a distinct kind from that on the Barberry here, and will enclose 2 or 3 diseased Berries. My Eyes do not allow me to use the Microscope much; and I use it with Reluctance: and therefore my observations are probably inaccurate. I have made a few Experiments; but they are of little Importance and certainly wholly indecisive. On the 10th. of this Month I placed on one of the Leaves of a Plant of Wheat which was perfectly free from disease, apparently, a sufficient Portion of the seeds and seed-vessels of Rust taken from a diseased and distant Plant of Wheat, to give a visible Redness to the Leaf. I examined it every day till the 15th, when it did not appear to have made any progress whatever: on that day I sprinkled the Rust with Water three or four times, and repeated the same Process during the four succeeding days; and yesterday I observed the spot covered with Rust, which is shedding its seeds. This would appear tolerably decisive; but I applied the Rust of the Barberry to three other Plants; and on two of them the same Effects were produced, and the Rust, examined by the Microscope, appeared precisely the same Plant. I must add, that, though greatly most abundant on the spots and immediately round them, where the seeds of the Rust were deposited, the disease appears slightly in different Parts of all the Plants, and therefore the Experiment is of very little value. I would, nevertheless, have inclosed a Part of the Straw on which the disease appeared to have been propagated from the Barberry; but a villanous jack ass

I keep has broke into the Place where my Plants were growing, and has swallowed Rust, Wheat, and all together.'

'Elton. Nov. 16th. 1805.

'Since I had last the Pleasure of writing to you, I have paid a good deal of attention to the Progress of Rust on some very late sowed Wheat and Oats: but the Result of my Experiments and observations has only led to make me doubt of every Conclusion I was previously disposed to draw. I am, however, almost satisfied that much Moisture, applied to the stem and Leaves when the Roots are ill supplied with it, will, in almost all Cases, bring it on. I think also that it sheds its seeds in ten days at farthest from its first taking Root in the Leaf or stem; and that, if Land be ploughed deep and sowed thin and early, the Crop of Wheat will rarely be affected. I have already informed you that I have, during the last few Years, always succeeded in raising as fine Crops of Pease for my Table in September as in the Spring, by previously soaking the Ground to a considerable depth with Water, and subsequently keeping it moist; and my wheat Crops, which are always sowed very early and thin, have never been affected by Mildew; tho' I can at any Time succeed in raising a Mildew Crop. The Mildew on the Barberry, I can not doubt, from what you say, to be a different Plant from the Rust on Wheat: nevertheless I have no doubt but that the same bad Culture that will bring on the Mildew on some Plants will produce the Rust on Wheat; tho' the parasitical Plants themselves may belong to different Genera.'

A book which has often been overlooked in the history of the rust problem is L. G. Windt's '*Der Berberitzenstrauch, ein Feind des Wintergetreides*' (1806), though de Bary mentions it in the account of his classical experiments on heteroecism (1865). The book is very rare, and, so far as I know, the only copy in this country is in the Banksian Library at Bloomsbury. There is, however, a translation in the Department of Botany with the title '*The Barberry-bush an enemy to winter corn, proved by observations, experiments and testimonies*'. Windt began his observations in 1804, not knowing of 'the bad reputation of the Barberry in Holland, England, and even in America... I thought my enquiries were new; at least matters of attention only in this neighbourhood'. The book mainly consists of a series of 'diaries, records and testimonies', from which the evil report of the Barberry appears to be by no means founded on vulgar prejudice.

Windt's work should receive mention in even the most summary historical account of heteroecism, for he has given a detailed and convincing account of the effect of barberry on cereals—particularly rye.

The PRESIDENT, expressing his interest in the matter brought forward by Mr. Ramsbottom, enquired whether copies of the book referred to by Mr. Ramsbottom and from which he had quoted were available in continental libraries.

Mr. RAMSBOTTOM replied that, judging from the fact that it was so very rarely mentioned, there could not be many copies available.

The following papers were read in title :—

Scientific Results of the Cambridge Expedition to the East African Lakes, 1930-1.—7. Algae. By FLORENCE RICH.

——. 12. Aquatic Heteroptera. By Dr. T. JACZEWSKI. (Communicated by Dr. E. B. WORTHINGTON.)

16 FEBRUARY 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 2 February 1933, having been circulated, were taken as read and confirmed.

The President reported the death of Sir Daniel Morris, K.C.M.G., for fifty years a Fellow of the Society, and referred to his services in connection with the agricultural resources of the British Empire.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—Robert Moyes Adam.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Bindiganavale Thirumalachar and Thengumpampil Kurien Koshy.

Taxonomy and Cytology. [Hooker Lecture.]
By Professor Sir William Wright Smith.

(Abstract.)

IN his introductory remarks the lecturer made reference to Sir Joseph Hooker, commenting on the 74 years of continuous work of that distinguished botanist and on the

importance, quality, and permanence of his publications, especially those dealing with the floras of areas within the British Empire. His methods were those of his time, and in the main he followed the accepted lines of systematic botany. The advent of the 'Origin of Species', his close friendship with Darwin and their intimate debate did not affect his broad general policy in systematic botany, a policy which was current throughout the nineteenth century. Investigations in other departments of botany did not influence systematic viewpoints to any marked degree. The systematist continued to use the old criteria. Some of the tools were sharpened to a finer point, but they were the same tools.

But in these days the progress of Genetics and Cytology has brought in new factors. The results of the new investigations penetrate deeply into the domain of the systematist. Moreover, the data so derived are of a character quite different from what taxonomists usually employ. But it is clear that we have in these data criteria of great significance for taxonomic studies. Their interpretation is not yet exact. The results are often conflicting, or at least divergent. Many genera have now been investigated cytologically—at least in part. Some show little diversity in their grosser cytological characters—others are remarkably irregular. A genus which has marked morphological divergence among its species may show negligible chromosomic variation, while in others the chromosomic variations may be quite outstanding. Consequently there is no evidence that morphological diversity in a genus is necessarily in a parallel relation with chromosomic diversity. The value of the chromosomic criteria for taxonomic work is a matter for careful investigation. The results will vary from genus to genus, and no general rule is likely to emerge. In illustration of the attempt to appraise the taxonomic value of the cytological criteria the genus *Primula* was chosen for this lecture. The many species of the genus have recently (1928) been enumerated, arranged in sections, and placed in their affinities in accord with their morphological characters. Subsequently, in 1932, Dr. Bruun of Uppsala worked out the cytological characters of all those available in cultivation. On the basis of these he has drawn up a taxonomic survey, and has contrasted his results with those obtained from morphological data only. As the species worked out have been numerous, the analysis is on a reasonably wide field. The genus has proved to be particularly favourable for both morphological and cytological investigation. Morphologically it can be divided into some thirty reasonably definite sections; cytologically the same is true. As in other genera, the results of the two lines of investigation show in the main a remarkable uniformity.

This is in itself an indication of the validity of the new line of attack and of the new criteria. But there are on several points divergences of opinion, and these divergences are of special interest as affording a means of contrasting the respective values of the morphological and of the cytological data. An impartial survey of these tends to the following conclusions :—

- (a) There are cases where the cytological criteria serve to solve taxonomic problems where morphologists have previously been in doubt or at variance.
- (b) There are cases where the cytological data challenge decisions of the morphologist—and with reason.
- (c) There are cases where the cytological data would appear to uphold relationships which the morphologist would decline to accept—and again with reason.
- (d) There is a general agreement in the two sets of data as to sectional values—this agreement is almost without exception. Where the analysis is carried beyond the sections, there is then a greater likelihood of divergence of view.

In a brief review of the morphological criteria used in the definition of the sections of the genus, it was pointed out that it was only rarely that these could be used absolutely—a reasonable latitude of interpretation being necessary. It would appear that the same is to a great extent true of the cytological criteria, for the number, size, shape, etc., of the chromosomes do not always give clear evidence when applied to taxonomic problems.

Several sections of the genus were illustrated on the screen, and comparisons were made between the conclusions arrived at by the morphologist and by the cytologist on their respective data. Instances of divergence of view were discussed in some detail.

It was also clear from the analysis that different sections of the genus (equivalent from the point of view of specific diversity) showed very varying degrees of chromosomal evolution. Some large sections were remarkably uniform; in others there were numerous instances of polyploidy; in certain sections aploidy was evident.

Doubt was consequently expressed as to the validity of using chromosomal divergence as a *measure* of difference between genera or as a means of dividing a large genus into several genera. Chromosomal divergence would certainly indicate usually that a line could be drawn between two groups—but it would not follow that even a marked difference would justify generic separation. Such separation would require to be based on the morphological evidence at the final arbitrament.

In conclusion, the importance of utilizing all available criteria in Taxonomy was emphasised.

Professor R. R. GATES remarked that Sir William Wright Smith had given a very interesting account of the relation between chromosomes and morphological characters in the genus *Primula* from the taxonomic point of view. He had shown that the grouping of the genus into sections corresponded in general with the chromosome numbers found by Bruun in the species in each group, and that the chromosomes were also useful as an additional taxonomic character in determining the position of species whose relationships otherwise were uncertain. It needed to be pointed out, however, that while the chromosomes were useful in furnishing additional characters for the taxonomist, yet their phylogenetic importance was much more fundamental than that.

The modern experimental work in botany and zoology had shown that the chromosomes occupied, as it were, a privileged position, for they were the basis of the morphological characters displayed by the organism. The substances they contain determine the metabolic processes, whose results are congealed and solidified, as it were, in the form and structure of the adult organism. Recognition of this fact necessitated the investigation of phylogenetic changes taking place not merely in the number of the chromosomes, but also in various details of their morphology, and further still and more fundamentally in the linkage relationships of the genetic characters which they determined.

In such genera as *Antirrhinum* it had been shown by the work of Baur and others that the various European species had apparently all undergone differentiation solely through gene mutations, since interspecific crosses gave ordinary Mendelian behaviour. In some other genera, such as *Oenothera*, the results of interspecific crosses showed that cytoplasmic differences as well as chromosomic differences existed between some of the species. How these differences in the cytoplasm of species had arisen was quite unknown at the present time, but it was evident that some species differed in their chromosomes or gene content, while others differed also in their cytoplasm.

As regards chromosome numbers, it had to be remembered that tetraploidy could occur independently in two unrelated diploid species, and that therefore two tetraploid species with the same chromosome number were not necessarily nearly related to each other. On the other hand, there was evidence, for instance in the cottons, that some at any rate of the Western hemisphere tetraploid species had been differentiated from a common tetraploid ancestor.

Other changes in chromosome number, such as the increase or diminution of one in the number of pairs, could perhaps be accounted for in the former case by non-disjunction of chromosomes at reduction division, as first described in *Oenothera*, and in the latter case (diminution) by the end-to-end fusion of two chromosomes. This has evidently occurred in certain insect genera and has been observed to arise in *Drosophila*. Transverse fragmentation of certain long chromosome pairs to form several small pairs had apparently occurred in such genera as *Yucca*.

Changes in genetic linkage showed, especially in *Drosophila*, that in certain species a whole section of a chromosome had become reversed. Visible chromosome changes were also found and analyzed genetically and cytologically under such names as translocation, duplication, and fragmentation. The study of the phylogeny of chromosomes was a great field, the investigation of which had only begun. Its results would help greatly in the analysis of specific relationships and in the determination of lines of phylogeny within a family from the taxonomic point of view.

Dr. E. J. COLLINS commented on the value of cytological research. Developed first as an aid to genetical studies, such work has become of increasing service to systematy. The ample material which Sir William Wright Smith kindly provided from the valuable collection of *Primula* species growing in the Royal Botanic Garden, Edinburgh, made it possible for Dr. H. G. Bruun to carry through a most comprehensive piece of research work on the cytology of the genus, and so to try out its worth in taxonomic studies. Dr. Bruun, now of the Botanical Institute of Uppsala University, received his early training in cytological methods at the John Innes Horticultural Institution, 1923-4, and published his 'Cytological Studies in *Primula*, with special reference to the relation between the Karyology and Taxonomy of the Genus', in April 1932.

Some 180 forms have been examined, including approximately 170 species and 10 hybrid types; of these Dr. Bruun is responsible for the original chromosome counts and figures of about 140 species, and gives confirmation of some 22 others. No other genus with such a wealth of 'clean' species had been examined on such a scale, and definite cytological types of nuclear structure, karyotypes, have been identified, and these have been grouped into karyoforms, and though, as Sir William Smith has stated, disagreement between taxonomist and cytologist about certain species occurs, yet the value of cytological studies for systematic work is confirmed.

Dr. Collins further recalled the chromosome investigations made in certain other genera, e.g. *Carex*, where a long

range of consecutive numbers (23–41) with only three missing figures (30, 36, 39) had been found, together with such other numbers as 9, 16, 18, and 56; in contrast, in *Lilium*, where the number 12 is constant throughout the species, it would be interesting to see how the expression of specific difference is manifested in the chromosome constitution, if at all (Linn. Soc. Proc., Feb. 4th 1932). In *Calochortus*, where, after a preliminary investigation, Newton reported that 'The doubtful correctness of the position of *Calochortus* in the Tulipeae is emphasized by the cytological differences that distinguish it from the other genera. The chromosome numbers found are 7, 9, and 10. Well-marked satellites occur in this genus and in conjunction with differences in size and attachment enable each chromosome in the haploid set to be distinguished individually' (Journ. Linn. Soc., Bot. xlvii (1927)). In the genus *Cistus*, so far as he (Dr. Collins) had found, the number of chromosomes was definitely 18, although the number of species examined was small. In the genus *Crocus*, in which he was particularly interested, research proved the existence of a wide range of chromosome numbers and Mr. Mather (Journ. Genetics, xxvi (1932)) had shown with this material that every haploid number between 3 and 15 is represented. Forms with odd chromosome numbers and aberrant types with trabants and satellites show that the genus is unsatisfactory from the 'purity of species' point of view, although of considerable value to the cytologist as a basis for advanced speculation in taxonomic and phylogenetic problems.

In conclusion, he thought it would not be doubted that there is something of value in the variation of form in nuclear constitution for systematic purposes, and further co-operation between systematist and cytologist would help to make the classification of some of the groups of plants less artificial; additional diagnostic characters of such an intimate nature as nuclear constitution would at least broaden the basis of classification, and this was all to the good.

Mr. IVAN M. JOHNSTON remarked that the number of species and individuals examined must be greatly augmented, and the extent of cytological variation between individuals must be determined before cytology can expect to become a shaping force in classification. It seems to offer a most interesting new source of information on plant-relationships, but at present its observations are so few, so restricted, so scattered, and so unchecked that taxonomists naturally consider them as only tentative, and at best merely indicative. The clues to relationships which it offers are most welcome, and it is hoped that cytologists will continue to give the apparent relational significance of their findings. Standley G. Smith (Bot. Gaz. xciv, 394–403, 1932) in his work on *Anchusa*

did this. The number of observations and of individual plants and species examined, however, as is so often the case in cytology, are too few and not sufficiently representative of the generic and subgeneric groups from the taxonomic point of view. Hence the investigation of *Anchusa* will be accepted merely as somewhat tending to substantiate the published taxonomic judgment, and not as validating it. The value of the clues to plant-relationship furnished by cytology are not to be disparaged. The recent work on *Yucca* and *Agave* by McKelvey and Sax (Journ. Arnold Arb. xiv, 76-80, 1933) is significant in this regard. Their study indicated a much closer relationship between these genera than is recognized in current classification. It substantiates a minority opinion one finds in systematic literature concerning the relations existing between the various groups of genera now separated as parts of the Liliaceae and Amaryllidaceae. According to this opinion, these families as now constituted are unnatural. The cytology of *Agave* and *Yucca* lends this support. A continuation of the investigations in the Liliaceae and Amaryllidaceae by the comparative cytologist may produce more evidence with similar impact, and so initiate, as well as substantiate, radical changes in the classification of the higher Monocotyledons. There are many reasons to believe that cytology will eventually become a most useful tool in rectifying and refining the details of plant-classification.

Dr. F. W. SANSOME made a few remarks and the lecturer replied, especially welcoming Dr. Collins's tribute to Dr. Bruun's work.

2 MARCH 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 16 February 1933, having been circulated, were taken as read and confirmed.

The President reported the deaths of Professor Carl Erich Correns and Dr. Johannes Schmidt, Foreign Members of the Society.

The President announced that the Council had unanimously nominated Dr. Stanley W. Kemp, F.R.S., as candidate for election as a Member of Council and as Secretary (Zoology), and that the General Meeting to be held on 16 March 1933 would be made a Special General Meeting for the ballots.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

Certificates of recommendation of the following candidates for Fellowship were read:—For the first time, in favour of William John Cooper Lawrence and Frederick Henry Reynolds.

The following candidates were balloted for and elected Fellows:—Leslie John Walker, Lawrence Root Waldron, Bindiganavale Thirumalachar, M.Sc., and Thengumparampil Kurien Koshy.

Leaf and bract forms of *Primula sinensis* and their inheritance. By Miss Dorothea de Winton.

PRIMULA SINENSIS was introduced into this country rather more than a hundred years ago from gardens in Canton, its wild form being still unknown. For some time only palm-leaved varieties were known, but we now have six distinct types of leaf, designated in these experiments, 'fern', 'oak', 'tongue', 'crimp' (a lesser and a greater), 'maple', and 'claw', besides one, 'ivy', which has been lost. Nothing is known of the origin of most of these types, but the more crimped form turned up in 1913 in the vinery of a private house; 'maple' appeared at the John Innes Horticultural Institution in an F_2 of a pure line of palm crossed to an extracted palm. 'Claw' also turned up at the John Innes two years ago as a single plant in a palm-leaved strain that had been inbred for six generations. The grandparent had been X-rayed, but as only a single plant of 'claw' appeared it is impossible to say if it was due to X-rays or not.

All these forms have mutated by loss from the original, and act as good Mendelian recessives, breed true and give a mono-hybrid segregation in F_2 on being crossed to the normal. No intermediates occur and the only hybrid generally distinguishable from palm is palm $\times$ crimp. Any two of these leaf-types crossed together give a palm F_1 , and in F_2 a normal dihybrid segregation in which the bottom recessive is a combination of the two original parents. It would be possible to combine all these leaf-shapes in a single family if enough plants were grown, but only one of the varieties of crimp could be included at a time as they are multiple allelomorphs.

Another Mendelian factor greatly increases the size of the bract. The normal bract bears a very small resemblance to the shape of the leaf, but when the bract is enlarged its shape closely follows that of the leaf. This factor is a Mendelian recessive to the normal, but there are three more or less distinct types of leafy bract whose genetical differences are not yet fully known.

The PRESIDENT thanked Miss de Winton for the trouble she had taken to bring together such an interesting collection of living plants for the illustration of her remarks. He presumed that the factorial constitution of the plants must be very complex to allow for other possible mutations which had as yet not made their appearance. He also wished to know whether the leaf mutations so far observed had appeared in pure lines as far as floral variations were concerned or from heterozygous stock.

Mr. A. J. WILMOTT, referring to the President's remarks, said that he had found it general that variations in leaf-form were reflected in the floral leaves, especially where relative breadth was concerned.

Professor R. R. GATES said that Miss de Winton had given a clear account of a series of allelomorphic mutations in leaf-shape, which had occurred in *Primula sinensis* over a long period of years. He asked whether, in crosses between the various types, a close approximation to the expected Mendelian ratios was obtained, or whether there were any deviations due to differential viability or other cause.

Mr. S. GARSIDE said that he had examined the anatomy of the 'claw' leaf and found it had enations from the upper surface, in the form of two crenate or lobed laminae arising one on each side of the midrib.

The enations stand more or less vertical to the leaf-surface; they have spongy parenchyma towards the faces which are in contact, and palisade cells towards their outwardly directed surfaces.

The enations are of the same nature as those described for *Phlox* by Worsdell ('Plant Teratology,' i. p. 201).

Prof. E. W. MACBRIDE congratulated Miss de Winton on her clear account of the mutations of leaf-structure encountered in *Primula sinensis*, and of the inheritance of these mutations when the mutant was crossed with the type. He alluded to the circumstances that the wild ancestor of *Primula sinensis* was unknown, that the garden species had been cultivated for many hundred years, and that the number and degree of abnormality of the mutations of any species was to some extent correlated with the length of time that it had been exposed to the abnormal conditions of garden soil. When, however, the garden varieties ran wild and were able to maintain themselves in competition with the wild species of the native flora the mutations disappeared and the wild type was restored. Of this one striking example had been given by Sir David Prain, who had observed that our garden *Calceolarias* were cultivated in the hill-stations of India, and there appeared in all the gay array of colours so familiar to us here—but that when, as often occurred, they escaped

from the gardens and propagated themselves on the bare hill-sides they all reverted to the small yellow form which was identical in colour and shape with the wild ancestor in Mexico.

This observation seemed to bear out the view supported by the late Dr. Johannsen that mutations were 'superficial disturbances of the chromosomes', disturbances which were produced by the unhealthy character of the environment and which persisted, and were inherited so long as the character of the environment remained the same—but underneath the mutations the original constitution of the species remained unchanged, and asserted itself as soon as a natural environment was restored.

A dodecapodous Pycnogonid. By Dr. Isabella Gordon.
(Exhibit.)

THE following is a summary of Dr. Gordon's remarks :—

The vast majority of the Pycnogonida (at least four hundred species belonging to some forty genera) have four trunk somites and four pairs of legs. In 1835 Eights described a decapodous antarctic form, *Decolopoda*, which was forgotten or regarded as an abnormality until its rediscovery in 1905. In 1904 a second decapodous form, *Pentanymphon*, had been described, and in 1910 still a third genus, *Pentapycnon*, was added. These three genera are not nearly related to each other, but each is very closely allied to a normal octopodous genus. At present five decapodous species are known, four of which are antarctic.

During his last antarctic expedition Sir Douglas Mawson obtained, in the region to the south of Kerguelen, the magnificent specimen now exhibited. It measures 20 inches from tip to tip of its outstretched legs, of which there are six pairs. Except for the possession of an additional trunk-somite and pair of legs, the species conforms to the definition of the genus *Decolopoda*.

Dr. W. T. CALMAN called attention to the interest of the decapodous and dodecapodous Pycnogonids from the point of view of phylogeny. He considered them to be specialized, not primitive, having been derived from octopodous forms. Once the stability of the octopodous condition had been departed from, the difference between decapodous and dodecapodous was of minor importance. Analogies were suggested among Elasmobranch and Teleostean fishes as regards the numbers of gill-arches and of vertebrae respectively. It was possible that the Pycnogonida as a whole had originated from an Arachnid stock through some analogous disturbance of metameric stability affecting the cephalic somites.

Dr. CALMAN also exhibited a cast of *Palaeopantopus*, described by Broili from the Lower Devonian of Rhenish Prussia, and regarded by him as a Pycnogonid. In spite of the great resemblance to a Pycnogonid in general form, its reference to that group could not be considered as beyond doubt. Should it be confirmed, however, it would show that the octopodous condition dated from a very remote period.

Dr. C. TATE REGAN :—It used to be considered that a high number of metameres was primitive, and that the general course of evolution was a reduction in number accompanied by differentiation. Those who work on classification now accept that an increase in number takes place just as often as a decrease. Dr. Calman has given an example from fishes ; it is clear that from fishes with 24 vertebrae, a number characteristic of many families of perches, have been derived others with more numerous vertebrae. The Flatfishes are a good example, *Psettodes*, the most primitive flatfish, having twenty-four vertebrae, whereas the other fishes of this group have an increased number, up to seventy, the increase being obviously related to the habit of swimming along the bottom of the sea by undulating movements. When fin-rays increase in number this also appears to be related to habits. In the Pycnogonids the numbers are small, and the addition of a segment is therefore a large change ; also one cannot see that it is of any advantage. In these respects it recalls the saw-shark *Pliotrema*, which differs from *Pristiophorus* and from all other Squaloid sharks in having six gill-openings and gill-arches instead of five. Here we appear to have examples of evolution by accident, a phenomenon which is difficult to understand.

Mr. G. C. ROBSON enquired if there were indications of additional neuromeres accompanying the extra legs in *Dodecolopoda*, and drew attention to the tendency for the standard number of arms in Decapod Cephalopods to be modified in various groups.

Prof. MACBRIDE asked Dr. Gordon concerning the twelve-legged species. The normal Pycnogonid has only eight walking legs. At which end of the series were the four extra legs put in ? It might be maintained, as was done by the late Dr. Bateson in a similar case, that when a meristic series varied in two related animals the whole series in one corresponded to the whole series in the other, and that it was impossible to equate any member of the shorter series to a definite member of the longer series. But undoubtedly this generalization would not always work. The normal starfish had five and only five arms, and this number was found in the earliest-known starfish in the Ordovician. But in two

existing families the number five had been largely increased, and in both it was perfectly possible to identify the original five arms amongst the multitude of arms which starfish of these families possessed. In the Solasteridae, which included our common Sun-stars abundant in the Firth of Clyde, the original five arms were first formed in the metamorphosing larva as an open hoop. This was true also of the normal starfish, and the two ends of the hoop became joined together to form a ring. But in the Sun-star a number of supplementary arms were budded off at one end of the hoop before the hoop became a ring; so that the additional arms might be said to be inserted in one interradius of the original five-armed starfish.

In another family, the Heliasteridae, not found in our seas, but common on the Pacific coast of N. America, the young starfish after its metamorphosis from the larva had only five arms. New arms were added as it grows in size, sprouting from various interradii until the full number of adult arms had been attained.

Mr. J. RAMSBOTTOM, referring to remarks by Dr. Calman and Dr. Tate Regan, said that in one of the main divisions of fungi—the Ascomycetes—the number of spores was almost always eight. When there was variation it was usually in a group of allied forms, e.g. Tuberaceae, Ascobolaceae, and Saccharomycetaceae. There seemed to be no evolutionary significance in the departure from the normal number of spores in the ascus.

Dr. CALMAN, in replying, stated that in the ten-legged species, and presumably in the new twelve-legged form, the ventral nerve-chain showed a corresponding increase in the number of ganglia. He did not think that the individual metameres could be equated in the way suggested by Prof. MacBride. It seemed more probable that in these animals the series of metameres, whether four, five, or six, corresponded as a whole.

Dr. G. S. CARTER, on behalf of the author, gave an account of this paper :—

Scientific results of the Cambridge Expedition to the East African Lakes, 1930–31.—13. Adaptation to aerial respiration in *Alma emini* Mich., an oligochaete from East African swamps. By Mr. L. C. Beadle. (Communicated by Dr. E. B. Worthington.)

ALMA EMINI is a small oligochaete which was collected in E. Africa by the expedition, in mud at the bottom of very shallow water. It is remarkable for the possession of a shallow groove on the dorsal side near the anus. It was observed

to expose this part of the body to the air above the water at frequent intervals. Histological investigation showed that the skin in this region is more vascular than that over other parts of the body, and the ectodermal epithelium higher. The muscle-layers below the ectoderm are also more developed in this area, perhaps in connection with their function of opening and closing the groove.

These observations, and the fact that oxygen is very scanty in the mud in which the worm lives, make it very probable that the groove is a respiratory organ, and the habit of raising the groove above the water is a means by which the worm lives in its dioxygenated habitat. The worm, therefore, resembles the species of *Drilocrius*, previously described (Journ. Linn. Soc., Zool. xxxvii, 379), both in the nature of its habitat and its adaptations to the conditions of the habitat.

The water-relations of plant cells. By Dr. Elizabeth C. M. Ernest. (Communicated by Prof. V. H. Blackman, F.R.S.)

It was shown that suction pressure rather than osmotic pressure was the determining factor in water-exchange of the plant cell, and that the value of suction pressure depended largely on the mechanical properties of the cell-wall; if the cell-wall was extensible the suction pressure might be of any value between zero and the full osmotic pressure, but if the wall was non-extensible the suction pressure was either zero or equal to the full osmotic pressure without intermediate values. The method of measuring suction pressure was described, and emphasis laid on the necessity for avoidance of the *section* method of obtaining cells in preparations suitable for microscopic observations for plant-cell physiology.

In thanking Miss Ernest for her paper the PRESIDENT enquired whether the measurements of extensibility of the cell-wall were always made on mature plants or on leaves in different stages of development. He presumed that in younger leaves the cell-wall might be more extensible.

Mr. J. C. WALLER asked whether Miss Ernest had considered measuring changes in volume of the *whole* leaf.

In reply, Miss ERNEST said that her experiments were always with mature plants: she thought that measurements of the whole leaf had been made in Czecho-Slovakia.

SPECIAL GENERAL MEETING

16 MARCH 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 2 March 1933, having been circulated, were taken as read and confirmed.

The PRESIDENT reported the death of Professor G. C. Bourne, who had been the Society's Zoological Secretary from 1912 to 1915.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—George Francis Scott Elliot, Thengumparampil Kurien Koshy, and Bindiganavale Thirumalachar.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of William John Cooper Lawrence and Frederick Henry Reynolds ; for the first time, in favour of Puthenparampil Joseph Gregory and Doris Richardson.

The Bye-Laws regulating the Election of Council and Officers having been read by the Assistant Secretary, the PRESIDENT declared the Ballot for a new Member of Council and a Secretary (Zoology) to be open, and voting began. The Ballot for a Member of Council was closed at 5.30 p.m. and for a Secretary at 6.0 p.m.

The PRESIDENT appointed Mr. H. W. Pugsley, Mr. H. N. Ridley, and Mr. A. W. Sheppard as Scrutineers of the Ballot.

Four zoological exhibits. By Captain J. G. Dollman.

1. A pair of Hippopotamus tusks presented to the British Museum (Natural History) by Mr. G. G. Feasey. The tusks came from an animal shot by Mr. Feasey in Nigeria, and are of special interest in that one tusk is normal and one shows extensive disease owing to an old fracture. The latter is probably the result of a wound received while fighting.

2. The skull of an elephant from the Gola Forest recently sent home with two other specimens to the Museum by H. E. the Governor of Sierra Leone. It was pointed out that this specimen was reported to be a Sierra Leone dwarf elephant, or 'Sumbi'. It represented, however, the same race of elephant as the specimen presented by the Governor some time ago, and which formed the subject of a previous communication to the Society. It was, undoubtedly, an immature individual, as the last molar was not in position and the sutures of the skull were open.

3. A collection of mammals recently presented to the Museum by Admiral Lynes, and collected by Mr. J. Vincent in Portuguese East Africa and Nyasaland. Attention was drawn to two mammals, an Elephant Shrew of the genus *Rhynchocyon* and a Squirrel of the genus *Funisciurus* which appeared to require description.

4. New Golden Moles from East Africa. This exhibit dealt with two species of Golden Mole, from Tanganyika Territory and Ruanda, belonging to the genus *Chrysochloris*, which appeared to be new. One of these had recently been collected together with some other mammals in the Mporota-Rongwe area in Tanganyika Territory by Mr. W. G. Cubitt-Currie.

Mr. JACK VINCENT said that the expedition from which he had recently returned was undertaken on behalf of the British Museum for a review of the avifauna of Portuguese East Africa, one of the few remaining corners of Africa which were little known ornithologically. Although a certain amount of collecting had been carried out from time to time in that country, this expedition was the first one of any magnitude confined solely to the exploration of the Colony of Mozambique, where the paucity of natural history investigation is accounted for in part, perhaps, by the bad reputation the country has held for unhealthy climate.

Almost all the specimens exhibited were obtained on Portuguese soil. Some fifty small mammals were secured, but they formed only a side-line, for the primary consideration was the collecting of birds.

He was most gratified to know that the specimens have been identified, and that something of interest was contained in this small collection, and also to hear that there should be two or three species new to science.

Captain Dollman's remarks on the new squirrel, the nearest relation of which appears to be a species confined to the Ruwenzori Mountains, raises a point of particular interest because it seems to point to the fact that the distinctive 'island-mountain' forms, which we know exist among birds, have a counterpart in the mammals.

The most interesting examples of these separate mountain forms, cut off from each other by intervening savannah-country, quite unsuitable for the movement of fauna peculiar to high mountain rain-forest, are found in the mountains of north-eastern Tanganyika Territory, and he had discovered a similar state of distribution among the mountains of southern Nyasaland and northern Mozambique.

Some of the most interesting specimens exhibited were obtained on the Namuli massif 15°-21 S., 37°-04 E. This is the highest mountain in Portuguese East Africa, and he had been able to explore it in considerable detail. The results of this exploration were of particular interest, since the mountain had been visited only once previously, in 1887, and many specimens of interest were obtained, especially of birds, in its high forests. The squirrels and jumping shrews were quite common there, and frequently, whilst he was quietly observing new and rare birds, they would approach quite closely, and were added to the 'bag'—indeed, the agitated movements of some of the squirrels in the giant forest-trees were often mistaken for the presence of a Turacou or some other similar bird. The giant rat was common in the forest also, and was sought for by his natives as a table delicacy.

Mr. W. S. ROWNTREE asked about the feeding-habits of the rodent mole. Was there evidence of any change in the feeding-habits? Had the creature ceased to be a mere gnawer?

Captain DOLLMAN, in reply, said that the various genera of Rodent Moles such as *Cryptomys*, *Georychus*, *Bathyergus*, *Tachyoryctes*, and *Heterocephalus* exhibit convergence with the Insectivorous Moles and the Marsupial Mole (*Notoryctes*). Their general form is similar, and their habits, as regards their burrowing propensities, are also similar, but their diet is widely different. The Rodent Moles, as is evidenced by their teeth, feed only upon vegetable matter, chiefly subterranean, such as roots, whereas the Insectivorous Moles exist largely upon worms and such small insects as they can devour and digest.

DISCUSSION ON MORTALITY AMONG YOUNG PLANTS AND ANIMALS

Seedling mortality amongst plants.

By Professor E. J. Salisbury.

THE simplest case is presented when competition is inter-specific, the seedlings of the species being unaccompanied by other types. The cases studied were monocarpic species, thus avoiding the complications inherent in polycarpic types.

A variety of species showed densities of seedlings ranging from under 100 per sq. decimeter to an average of 1200

seedlings per sq. decimeter in a growth of *Dianthus prolifer*. The number which survived the seedling phase was in every instance under 5 per cent. of the original population, and in an instance of *Verbascum thapsus* a seedling mortality of over 99 per cent. was recorded.

The meagre data of a quantitative character is partly attributable to the dominance of a theoretical quasi-mathematical concept that for every parent that perishes only one of the offspring will survive. This concept, whilst true for a long period, or perhaps of a sufficiently large area, conveys a totally false impression of relative stability in numbers, and tends to obscure the fundamental biological fact of fluctuating populations. An example of the extent of such fluctuation is furnished by the occurrence of *Cnicus palustris* in a woodland area with an abundance of under one individual per square metre, whereas in the year following an abundance of 243 plants was recorded. These individuals, though small in size, attained maturity and fruited.

The importance must be stressed of the fact that in the instances studied the survivors from seedling mortality almost without exception attained the flowering stage and produced viable seed. Investigations show that on the same soil the range in size of the same species may be very great, but it should be noted that even depauperate individuals usually flower and fruit. Tests carried out with a variety of species showed that the seed from the most depauperate individuals was as viable, and gave as high a percentage germination, as those saved from the largest individuals. There is thus no evidence that strains which may be represented in these depauperate plants are eliminated by failure to produce offspring, either through selective pollination or selective viability.

There was hence no evidence of selection in the later stages of development. Whilst deaths at this later stage may be due to catastrophic causes, and here as earlier random mortality may occur, any natural selection that does occur must be practically confined to the seedling stages. Comparison of growths of differing densities of seedlings seems to indicate that in general the greater the density of the original seedling population the lower the proportion, and frequently the absolute number, of survivors, thus again emphasizing the dominance of the seedling stage in determining the extent of mortality.

It has always been assumed as more or less axiomatic since the time of Darwin that competition is greatest between individuals of the same species. But in species which occupy the same 'niche' the reverse is probably the case, since individuals of the same species are so well balanced in their

biological equipment that mortality is actually less, and as we have seen many individuals may survive though diminished in vigour from mutual competition. When the competition is between different species, however, or between different strains of the same species, the difference in their biological equipment may enable one or the other to gain the mastery, and hence to survive. Data obtained from the study of *Salicornia herbacea* and *Suaeda maritima* growing intermingled appear to show that the more one or other species preponderates the greater the total surviving population tends to be, and, similarly, when mixed communities of *Statice binervosa* having similar densities of population were compared, the number of *Statice* seedlings surviving decreased with the increasing density of other species, and not with the density of their conspecific competitors.

Here, too, in these mixed communities the mortality appears to be almost entirely a feature of the seedling stage, and the negative correlation as to survival just noted between one species and another, as distinct from individuals of the same species, is indicative that this is due to a qualitative distinction and not to mere random mortality.

Mortality of plants is therefore seen to be very high, and practically confined to the juvenile stages, though the period of mortality is more prolonged in perennial species. It is reasonable to suppose that whilst this mortality will include deaths of a 'random' character, it will also include any types, whether species or strains, which are less well equipped for survival. Such differences are probably qualitative rather than merely quantitative, and may well involve a group rather than a single character. There is no satisfactory evidence of selection at later stages, and indeed even the very depauperate individuals produce offspring.

Comparisons between offspring raised from seed and planted out soon after germination and those raised from similar seed samples, but planted out after the incidence of juvenile mortality, appear to warrant the conclusion that those seedlings which perish at least include types which differ in kind from those which survive, and thus indicates that the mortality is at all events in part selective.

If selection takes place when the morphological characters are so little differentiated that species of the same genus are often well-nigh indistinguishable, it would suggest that the morphological characters of the adult are perhaps the necessary concomitants of the characters upon which natural selection operates, and are only indirectly selected themselves. The actual characters which determine mortality or survival may be entirely physiological, though linked, it may well be, with the morphological and other attributes of the adult condition.

Dr. R. A. FISHER said that Professor Salisbury had drawn an extremely important conclusion from his original observations and original thought on the mortality of seedlings—the conclusion, that is, that the absence of mortality, which he believed to prevail between the end of the seedling stage and the completion of reproduction, precluded the action of natural selection during this period, and therefore prevented its acting on any of the adult characters of plants. The speaker would suggest, however, that, accepting entirely Professor Salisbury's views on questions of fact, such an inference could only be drawn from the facts adduced, by arbitrarily confining the action of natural selection to a differential death-rate, and by defining death in a sense appropriate to the higher animals, but not so appropriate to plants, namely, as the elimination of the whole organism.

In agricultural research considerable attention was now given to the history of the population of plants, which constitutes a growing crop, and a group of eight stations at present co-operated to carry out routine observations, by the sampling method, on fields of wheat. These data show from year to year, with some precision, the plant-number attained at its maximum, a few weeks after its first appearance above ground, in relation to the number of seeds sown and to the number which survive to enter into the second stage of the wheat plant's life, by forming the tillers, or shoots, which may ultimately bear ears.

From the beginning of April no further record of plant-number was taken, partly because the plants at this stage were difficult to separate, but principally because from this stage the shoots constituted the more important units. The shoots increase in number by tiller formation, and pass a maximum about the middle of May; a large number of shoots turning yellow, withering, and forming no ears. We speak of this as the death of so many tillers, though probably there may be little or no elimination of whole plants at this stage. In Professor Salisbury's sense there may be no elimination by death, and therefore no possibility of differential survival. But there is manifestly differential growth, and this, if we were dealing with a genotypically mixed population, is all that would be needed to enable the adult characters to be modified by natural selection.

With respect to the wild plants discussed by Professor Salisbury, he had stressed the necessity of showing that, after the dangers of the seedling condition were passed, all plants survived to complete their development and to produce viable seed. But it was not enough to show that all produced some viable seed—it was necessary, if selection were to be excluded, that all should produce equal quantities of equally

good seed. It was evident from Professor Salisbury's data that this condition was far from being fulfilled. He had shown that depauperate plants, bearing only a single capsule, were to be found growing side by side with luxuriant individuals bearing over 300 capsules, and such a difference represented an intensity of differential survival about 50 times as great as would be exhibited by a differential death of 10 per cent. of the plants.

It was natural that we should think and speak in terms appropriate to the higher animals; and, because a rat or a fish, if subjected to conditions which precluded its normal development, would usually die outright (rather than become a depauperate rat or fish, capable of normal reproduction, but with only one-hundredth the fertility of a normal animal), we are apt to speak of differential survival as the condition for natural selection in the growing period of animals. None the less, as Professor Salisbury's work had shown, it would probably be more appropriate in the case of many plants, to lay all the stress upon differential growth.

The PRESIDENT, pointing out the interest of Professor Salisbury's remarks, referred to the work on the mortality of seedlings that had been carried out at the Welsh Plant-breeding Station at Aberystwyth. It had been shown by Professor Stapledon and Mr. Jenkins that in several grasses *Lolium perenne*, *Phleum*, and *Dactylis glomerata* self-fertilized plants produced a large number of albino seedlings and others sharing varying degrees of chlorophyll deficiency. These naturally died off at an early stage. Mr. Jenkins had also discovered two lethal factors in seedlings of normal green colour, so that it is obvious that in these cases there was considerable mortality of seedlings. The establishment percentage of viable seedlings was sometimes as low as 9 per cent. in the Italian Rye grass and Cocksfoot grass. Dr. Tincker had shown that in Oats the drying of the seeds promoted greater rapidity of germination and greater vigour of the seedlings, and the same was true of larger seeds. In both cases the establishment percentage was increased. Some of the experiments carried out at Aberystwyth confirmed Professor Salisbury's contention that competition was greater among seedlings of different plants than among seedlings of the same species. In mixtures of seeds it was found that the presence of Rye Grass depressed the soil establishment both of Cocksfoot and Meadow Fescue Grass.

Dr. E. S. RUSSELL called attention to the great fecundity of most sea-fish, and the consequent enormous mortality, which affects principally the eggs and larvae. It has been shown by Wollaston that the total number of eggs produced in the spawning season of the plaice in winter in the southern

North Sea was in 1913-14 some five million million. Between spawning and hatching the eggs suffered a mortality of 70-90 per cent. Other cases of heavy mortality in eggs are known, notably in the herring, whose demersal eggs are eaten in vast quantities by haddock and other fish. Mortality in fish-larvae, especially at the critical stage when the yolk-sac has been absorbed, is known to be high, and it is probably in these early weeks that the relative success or failure of the year's brood is determined, giving rise to the fluctuations in abundance that are characteristic of most fish. Little is known with certainty as to the causes of this early mortality; enemies, shortage of planktonic food, unfavourable hydrographical conditions, abnormal currents, are probable factors. The probability is that the mortality is non-selective, but as to this the evidence is very scanty. So far at least as bottom-living fish are concerned, mortality is considerably reduced in rate after larval and postlarval life has been passed through, and the young fish have settled down on the bottom. Mortality in fish of catchable size is mainly a function of intensity of fishing, and the rate of mortality due to this cause may be 50 per cent. per annum or higher.

Mr. O. W. RICHARDS (Visitor) said mathematical treatment of the trends of animal populations is perhaps only justifiable when applied to very large numbers over a considerable period of time. But it does at least allow us to make the simple deduction that with a 1:1 sex-ratio, there must, if the population is to remain stationary, be a death-rate of 90 per cent. if twenty eggs are produced. Most insects lay more than 100 eggs, and the death-rates necessary for stability lie between 95 per cent. and 99.9 per cent. Investigations of insects in nature suggest that parasites of the early stages alone often account for a 90 per cent. mortality. The effects of this particular cause of death are relatively easy to estimate, but other causes, such as the attacks of predators or climatic severity, while known to be important in many species, are not yet possible to evaluate quantitatively. It must be expected, however, that most of the death-rate should fall on the early stages, otherwise the available food would be used up before any individuals succeeded in coming to maturity. This type of wasteful intraspecific competition is, in fact, known to occur in the blowflies, which are probably rather exceptional.

Since we cannot as yet estimate the gross death-rates due to various factors, still less can we distinguish between the mortalities of different genotypes within a species. The study of the incidence of mortality amongst insects therefore, throws extremely little light on whether a selective process is at work in nature or not. A distinction must be drawn between random mortality, which is almost certainly very

great and destroys all genotypes impartially, and a selective death-rate, which, even if at a low rate and acting after the random mortality has taken its toll, might still have large evolutionary effects. Before we can establish the existence of, say, a 1 per cent. selective death-rate, a great advance will be required in our technique of estimating animal populations.

Mr. J. RAMSBOTTOM said that in considering the problem of the death of seedlings one may ask the usual colloquial question, 'What do they die of?'. So far we are certain only that they do not die of old age. This, however, is the only natural form of death in healthy plants; death before the allotted span may always be regarded as accidental, whether sudden or otherwise.

What are the possibilities of accounting for this unnatural death? Is it constitutional, something that prevents a seedling continuing to live beyond a certain stage or only so far as it is nourished and matured apart from competitors? What are the symptoms of death? Is death due to physical overcrowding by its brethren or other plants, inability to obtain food against competitors, or to the attack of parasites?

We know that there are seedling diseases, some of which cause epidemics, e.g. it is not possible to grow onions in the U.S.A. because of the onion smut, except at temperatures higher than 29° C., when the smut spores cannot germinate. There are also diseases which take a far less spectacular toll. In these immunity is often constitutional.

On the face of it one would be inclined to assume that, apart from parasitic disease or accident, death of seedlings must be due to starvation—the inability to obtain the necessary food.

This inability may be due not only to physical inability, but to the necessity of a symbiont. Seedlings of trees will sometimes die if the soil-conditions are unsuitable for their mycorrhizal fungus: this he had known to occur in beech. The starvation may occur at an earlier stage still, as in orchids where the fungus is necessary for germination. Here we can—though hardly in Banquo's sense—'look into the seeds of time and say which grain will grow and which will not'. Darwin calculated that the progeny of *Orchis maculata* would cover the globe after three years*, but probably few present

* '... Estimating in the same manner the smaller seeds of *Orchis maculata*, I found the number nearly the same, viz., 6,200; and, as I have often seen above thirty capsules on the same plant, the total amount would be 186,300. As this Orchid is perennial, and cannot in most places be increasing in number, one seed alone of this large number yields a mature plant once in every few years.

'To give an idea what the above figures really mean, I will briefly show the possible rate of increase of *O. maculata*: an acre of land would hold 174,240 plants, each having a space of six inches square,

had ever seen a seedling in nature. If the appropriate fungus is supplied to seeds in a culture flask they sprout like cress, forming a sward of healthy seedlings which will grow in that condition for months.

Mr. G. C. ROBSON hoped that Professor Salisbury's paper would lead to more attention being given to the question as to how presumed selective agencies act in nature. Exact evidence is needed, especially about invertebrate animals, on the causes of death and the age at which they become operative. We have very little knowledge as to the relative importance of catastrophic destruction as opposed to the annually recurrent mortality. He gave some instances of the effect of these from Mr. Stephen's work on the Mollusca of the Clyde Estuary. He felt that before it is possible to decide if natural selection is operative to any important degree, some kind of integration of the effects of all the lethal factors is required.

Dr. MARGARET BENSON also spoke.

Dr. W. T. CALMAN called attention to the fact that, in the Lobster, by far the greater part of the death-rate must be concentrated in the larval stages. Once the metamorphosis had been completed and the bottom-living 'lobsterling' stage had been reached, the death-rate, although not reduced to zero, must fall to a very low figure.

Prof. SALISBURY, in replying, stated that the depauperate plants produced viable seed which appeared to be in no way inferior to that from vigorous plants, and the offspring of these depauperate individuals were often quite as vigorous as those from seed of large plants and produced similar amounts of seed. But even if the small seed output as compared with normal plants did materially prejudice the survival of the races represented by the depauperate individuals, it is nevertheless true that their depauperate character appears to be determined at the juvenile phase so that we are again driven back to consider the plant at this phase in relation to survival.

The actual cause of mortality was difficult to ascertain, since, by the time it was possible to distinguish the individuals which would perish, no distinction could be made between that which was primary and that which was secondary.

and this would be just sufficient for their growth; so that, making the fair allowance of 400 bad seeds in each capsule, an acre would be thickly clothed by the progeny of a single plant. At the same rate of increase, the grandchildren would cover a space slightly exceeding the island of Anglesea; and the great grand-children of a single plant would nearly (in the ratio of 47 to 50) clothe with one uniform green carpet the entire surface of the land throughout the globe.' ('Fertilisation of Orchids,' pp. 277-78.)

A number of the seedlings examined showed fungal infection, but whether they were weakly because they had been infected or infected because they were weakly it was not possible to determine. In other instances there was no external sign as to the cause of death, which appeared to be due to some obscure physiological cause. In one strain of *Delphinium* some cream-flowered individuals with the 'brown-bee' centre were obtained from amongst seedlings 'picked out' at a very early stage, whereas from the control culture 'picked out' later no such plants resulted. That these cream-flowered plants were physiologically weaker was shown by the fact that all of them subsequently perished at a later stage.

The Scrutineers of the Ballot, who had retired at the appointed times with the voting lists, having completed their scrutiny, reported to the PRESIDENT, and he declared that Dr. STANLEY W. KEMP, F.R.S., had been unanimously elected a Member of Council and Secretary (Zoology).

GENERAL MEETINGS

6 APRIL 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 16 March, 1933, having been circulated, were taken as read and confirmed.

The PRESIDENT welcomed Dr. STANLEY W. KEMP, the new Zoological Secretary.

The PRESIDENT reported the deaths of James Groves, A. R. Sanderson and E. W. Mayhew, Fellows of the Society.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted:—Leslie John Walker.

The PRESIDENT announced that the Linnean Medal would be awarded this year to Professor ROBERT CHODAT of Geneva.

Certificates of recommendation of the following candidates for Fellowship were read : For the second time, in favour of Puthenparampil Joseph Gregory and Doris Richardson : for the first time, in favour of William Stephenson.

Certificates of recommendation of the following candidates for Foreign Membership were read for the first time :—Dr. Elmer Drew Merrill, Dr. Erwin Baur, Professor Adolf Pascher and Professor Filippo Silvestri.

Certificates of recommendation of the following candidates for Associateship were read for the first time :—Frederick James Killington and Thomas Sheppard.

The following Fellows nominated by the President as auditors for the Treasurer's Accounts for 1932-33 were elected by show of hands :—

Representing the Council : Miss E. M. Wakefield.
Mr. J. R. Norman.

Representing the Fellows : Mr. H. W. Pugsley.
Mr. D. J. Scourfield.

A revision of *Lobostemon* Lehm., and a discussion of the Species Problem. By Mrs. Margaret R. Levyns. (Communicated by Miss E. L. Stephens.)

SIR ARTHUR W. HILL gave an account of this paper, of which the following is an abstract :—

The species of *Lobostemon*, a South African genus of Boraginaceae, have long been recognized as being difficult to classify, and to remedy this much field and herbarium work has now been carried out. Although very nearly related to *Echium*, and by some botanists regarded as a section of that genus, it is here more precisely delimited and considered to be endemic to extra-tropical southern Africa.

Lobostemon is regarded as an advanced member of the Boraginaceae, and it consists mainly of shrubs or under-shrubs, usually scabrid-canescant and sometimes armed with spine-like hairs, and with scorpioid inflorescences of mostly blue flowers. Twenty-eight species are recognized, several of the previously so-called species having proved to be natural hybrids or forms due to varying habitats. They are arranged in five well-marked sections, determined mainly by the composition of the inflorescence, the shape of the corolla, the relative length of the stamens, and the degree of development of the staminal scales. The presence of these scales distinguishes *Lobostemon* from *Echium*, whilst a new genus is described, which is herbaceous with tufts of leaves arising

annually from an underground stem, the inflorescence having a bottle-brush-like appearance, the stamens, as in *Echium*, without the scales at the base.

A cytological investigation of about half the species of *Lobostemon* and of all the species of the new genus shows the basic number of chromosomes in both genera to be seven.

Appreciation of the early work of Buek (1837) is expressed, his account of the genus being remarkably good considering that he investigated only herbarium material. Later workers have unfortunately rather obscured the true relationships of the species by the neglect of floral structure, and by laying emphasis on vegetative features which have since proved to be variable in the field.

The species problem, with special reference to *Lobostemon*, is discussed, and it is shown that Vavilov's Law of Homologous Series in Variation is applicable.

Detailed descriptions of the two genera and all the species is given, together with their synonymy, and specimens in the principal European and South African herbaria are cited in full.

The PRESIDENT expressed his personal interest in Mrs. Levyns's paper, remembering the handsome appearance of the *Lobostemons* he saw on the veldt when visiting South Africa in 1905. He enquired whether in passing over from radial to bilateral symmetry the flowers developed an anterior lip or a posterior hood?

Mr. A. J. WILMOTT suggested that the zygomorphy in *Lobostemon* might be similar to that in *Echium*, where the enlarged lower petals served as an alighting platform for insects. He remarked that late-continued growth of inflorescences, leaves and hair-bases (with whitening and increasing asperity) was frequent in other genera of this family. He pointed out that the corolla scales in some Boraginaceae were hollow, opening to the outside of the corolla and presumably being invaginations, and suggested that possibly examination of their structure might indicate a similar origin when they were not hollow.

Mr. J. RAMSBOTTOM said that the suggestion that heat is likely to be a factor inducing mutations is interesting, as it recalls the experiments of Barnes, who induced saltations in several moulds by submitting them to heat.

Evolution in light of the incidental records of Taxonomy. By Professor W. H. Longley.

THE records specified are dates when currently accepted species of organisms were named, those when specimens of each—as nearly as may be determined—were first collected,

and what is anywhere set down regarding their ranges. The number of species in each recognized genus should also be included.

But dates of naming are in some way dependent upon time of finding, finding upon area occupied, and this upon the play of species on species, and of the environment on all in the very process in which all are made. If the nature of the dependence in each instance might then be made out, it appears to follow that an improved understanding of what is involved in evolution should result.

This conclusion holds, however, only if the species to which the records refer are for the most part groups given by nature, groups objectively and not merely subjectively limited. And the same may be said for the genera. The validity of the taxonomist's conception of genera and species must therefore be established first of all.

For our present purpose it is not entirely satisfactory to rest our argument solely upon the informed opinion of systematists themselves, though that is undoubtedly with us. This argument is addressed to biologists of varied interests and experience, and for the most part unacquainted fully at first hand with the problems and practice of working taxonomists. It is on this account clearly desirable to give it the broadest possible foundation.

It is proposed, then, to assume at first no more than that the genera and species of the taxonomic record *may* in fact correspond roughly at least with groupings given by nature. It is then in order to analyze statistically any available body of numerical data regarding these groups. If the analysis yields, as it does, only conclusions to be come at in other ways generally approved, it is also in order to maintain that the original assumption is sound and the method of analysis legitimate.

Omitting reference to details available elsewhere (Proc. Sixth Int. Cong. Genetics, ii, 120-123, 1932), it needs only be stated here that the conclusion seems clearly enough indicated that species of small genera upon the average occupy small areas, and those of large genera large ones.*

But, so far as we are aware, there is no more reason to suppose that the first species of a genus in ability to hold ground in competition with other species was in its own day—or still is, if it still lives—less competent than the second or any other arbitrarily selected, than there is to suppose that of a large number of soldiers drawn up in files at random the average height of the first man in each is greater or less than that of the general average for the group. And, if this be granted, the species of small genera—again upon the average—are

* On page 121, 7th line from the bottom, read, 'The species of large genera are found earlier than those of smaller'.

descended from ancestors which had little success, and those of large genera in living faunas and floras from ancestors which had upon the average much success in holding their own in competition with other species.

But if species through variation give rise at all to other species, evolution is a fact. And if ancestral species upon the average produce species of their own grade of ability, clearly what may happen in evolution is conditioned by the genetic composition of the parent: heredity is a factor in evolution. And, finally, if what may be called a poor inheritance is likely to entail an outcome in evolution differing from that entailed by a better one, a differential admittedly exists which brings in struggle and survival of the fittest in an obvious way.

But this is only to say that analysis of the incidental records of taxonomy leads to the conclusion most commonly reached by palaeontologists, anatomists, embryologists and others in their special fields. For no one denies that no evolution is possible unless heritable variations occur, and the occurrence of some processes of weeding out of variants upon a selective basis is almost as generally admitted.

Taxonomy, therefore, seems justified in her basic assumption that organisms when classified fall naturally, and for objective reasons, group within group. And her records, by no means free from error, in addition to whatever merely utilitarian merit they may have, must be admitted to possess besides the supreme value of fundamental data of science.

Dr. J. C. Willis, as is well known, some years ago discovered that when the genera in any great natural group of organisms are plotted against the number of their species they give always a curve of the same general form. They give actually curves which grow more and more alike as knowledge in the several groups grows more nearly complete. They owe their likeness to the fact that they are moving toward the same limiting form.

Dr. Willis's discovery was based upon statistical analysis of the incidental records of taxonomy, and has the validity of generalizations obtained from such data by what seem dependable methods. It is to him we owe our first evidence that the process of differentiation of genera and species in all great natural groups occurs according to law.

Why this should be so may be stated briefly: Upon a foundation of fact empirically determined and summarized in the familiar gas laws the kinetic theory of gases is established. According to its terms a normal gas is a system composed of ultramicroscopic units active and acting at random upon one another, units incapable of reproduction and variation. It is the typical 'kinetic system'. But there is no reason why there might not be systems of units active

and acting at random one upon another, and possessing the power to vary or to reproduce, jointly or severally. Such kinetic systems do in fact exist.

Glowing gases are systems composed of units active and acting upon one another at random, variable units incapable of reproduction. Populations composed of a single sort of organism, growing as populations of flies are grown in experimental cultures for the specific purpose of discovering their statistical law of increase, are as definitely systems composed of units active and acting upon one another at random, for from their law of growth laws of the form of the gas laws may be derived by inspection ('Science', lxxv, 248-250, Feb. 26, 1932). Their units are capable of reproduction, but may be regarded as lacking effective power of variation, at least within the life of the experiment.

Recall the few reptilian species of the Permian, the many first, and then the multitude, of species that followed. The sum of the processes by which they came into being constitutes, as one may care to describe it, either the evolution of the Reptilia or the differentiation of a reptilian population in the earth. But the population so produced is not like the population of flies developing in culture bottles, or of men developing in a continent. It is not composed of a single sort of organism. It is a compound population, a species population or population of populations.

But if simple populations are kinetic systems growing according to law when conditions are stable, and tending always to grow according to law no matter how variable the conditions under which they grow, it is scarcely to be doubted that that process of differentiation of a compound population which evolution is should also occur according to law.

We know enough, indeed, of the conditions under which their differentiation occurs to be able to indicate what form the curve of genera plotted against the number of their species should assume in them, when they are large enough to lend themselves to analysis satisfactorily: and the form of the curve deduced from theoretical considerations is the same as that toward which Dr. Willis's empirical curves are moving.

In conclusion, it appears that evolution theory is population theory, and population theory kinetic theory. The law of evolution, the law of growth and the secondary laws of populations have the same validity as the laws of gases. All alike are statistical laws, laws of kinetic systems, and as a group are related to kinetic theory broadly conceived in the same way that the gas laws themselves are related to kinetic theory as usually and narrowly restricted.

Prof. E. W. MACBRIDE said that he had listened to Prof. Longley's paper with great interest. Prof. Longley had been so kind as to call on him at the Imperial College

and explain the general purport of his forthcoming paper at the Linnean Society, so that Prof. MacBride was able to follow the paper closely.

Prof. Longley had sought to correlate the date of the 'discovery' of a genus with its distribution and to draw general conclusions as to the bearing of this date, and the number of species which a particular genus contained on the nature of the evolutionary process. The argument was statistical, and Prof. MacBride had no doubt that Prof. Longley's statistical computations were perfectly sound. But he was reminded of a saying of the late Lord Balfour that there were three grades of lie, viz.: (a) the lie simple, (b) the condemned lie, and (c) statistics. Unless the units with which statistics dealt were fixed and equivalent, statistical computations were the most delusive form of reasoning. Prof. Longley's units were species and genera, but both species and genera were ill-defined bundles of varietal forms, the limits of which were determined by the psychological bias of the naturalist. In his own favourite group, viz. the Echinodermata, the old well-known genus *Echinus* had recently been split up by Mortensen into four or five genera, on grounds which other naturalists thought quite unconvincing. Similarly, the old genus *Asterias* had recently been dismembered, and one of its best-known species, *Asterias glacialis*, was now placed in a new genus, *Marthasterias*. Of what significance was the 'discovery' of the genus *Marthasterias*? On the other hand, many naturalists were convinced that a large proportion of so-called species were varietal forms, and Major Flower, in his recent revision of the Mammalia contained in the Zoological Gardens, had abolished a great many species.

When one considered facts like these it seemed to him impossible to draw conclusions as to the nature and course of evolution from the data submitted by Prof. Longley.

Dr. G. P. BIDDER desired much more mathematics in biology, particularly of Dr. Raymond Pearl's mathematics, but suggested danger in the application of Professor Longley's interesting analogy to the varied laws which govern diffusion of motile species above the rank of *virus*. Comparison of gas laws might be helpful in such radiating and colliding distributions as the spread of elms by suckers, or of the sponge *Tethya* (*Donatia*) by gemmules; but movement of the individual is not random in homogeneous populations of flagellates, copepods, North Sea plaice, Atlantic eels and their larvae, nor in the migrations of our Aryan ancestors: in all these instances common response to stimulus tends to parallelism of path. Consequently there are few collisions, and nervous coordination tends further to avoid collision between members of the same shoal; and from a collision induced by rut, or cannibalism, one individual, alone emerges.

With comparative absence of collision, distribution in the occupied area rarely grades in density, as in gases, from centre to periphery according to the curve of error: animals who feed round their homes tend to a uniform density of population regulated by combat (e. g. robins). From other causes the distribution is even more different from gas law in the 'fairly ring'; where the 'occupied area' is empty, fungi exist only on the circumference, and radius increases in the ratio of time elapsed instead of the gas-law square-root of the time. Behaviour as to density, in most diffusing animal populations, is opposite to that in a diffusing gas: among colliding gas-molecules rate of spread varies directly as distance between molecules, but a sparse population of motile animals has no stimulus to further scattering; we see rate of spread greatest when population is most dense among the parallel-moving bees, bison, lemming, cod, and locusts.

Pearl's number of *Drosophila* in a litre is a specific character, not true of sparrows, bluebottles, or sandflies; therefore not comparable with Avogadro's number of molecules in a c.c., which is true of every gas, whatever the weight or structure of its molecules. Pearl found the rate of increase of the bottle population, related to percentage present of the full *Drosophila* number, in inverse ratio; as pressure of a gas is related to volume, but also as electrical resistance to transverse area, energy of a ripple to distance from disturbance, and, approximately, rate of growth to age of baby, and weight of young plaice to density of population. The last of these comparisons possibly offers more profitable analogy than the first.

Hydrolysis of starch in the stomata by the action of polarized light. By Dr. E. S. Semmens.

THAT polarized light has a hydrolyzing effect on starch in the mesophyll of the leaf, was shown at the meeting of this Society on 30 April 1931. This hydrolysis is equally striking on the starch in the guard-cells of the stomata, and affords a simple explanation of the diurnal opening (morning and evening) observed by Lloyd, Loftfield, Weber, and others.

The results of experiments shown on accompanying microscope slides were of three kinds:—

(1) Exposure of a portion of a *growing* leaf (e. g. Hyacinth) behind a Nicol's prism, having a wide cork rim.

(2) Exposure of a strip of epidermis on a microscope-slide mounted over a Nicol's prism, controls being placed over ordinary non-polarized light and in darkness.

(3) Exposure of whole living plants (e. g. young *Tropaeolum majus*) in separate chambers for three days.

(a) in light polarized by reflection from a sheet of ferrotype, covered by glass; (b) in ordinary light of equal intensity, reflected from rough white paper.

The experiments described indicated clearly that the polarized light, produced either by reflection from the sky or from a shiny leaf surface, is the main factor in causing the opening of stomata.

On a clear day, the early morning and late afternoon vertical sky light is strongly polarized, starch in the guard-cells is hydrolyzed, sugar is increased, and the maximum opening recorded by former observers is produced. This increased sugar is partly polymerized to starch in the bright mid-day sunlight, turgor diminishes and partial closing of the stomatal aperture takes place.

The following paper was read in title:—

Scientific Results of the Cambridge Expedition to the East African Lakes, 1930–31.—13. Crustacea Macrura (Prawns). By ISABELLA GORDON, D.Sc., Ph.D.

27 APRIL 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 6 April 1933, having been circulated, were taken as read and confirmed.

The PRESIDENT reported the deaths of Spencer Henry Bickham and Mudumalakurti K. Venkata Rau, Fellows of the Society.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

Certificates of recommendation of the following candidates for Fellowship were read:—For the second time, in favour of William Stephenson; for the first time, in favour of Violet Margaret Grubb.

Certificates of recommendation of the following candidates for Foreign Membership were read for the second time:—Dr. Elmer Drew Merrill, Dr. Erwin Baur, Professor Adolf Pascher and Professor Filippo Silvestri.

Certificates of recommendation of the following candidates for Associateship were read for the second time:—Frederick James Killington and Thomas Sheppard.

Convincing evidence in favour of Organic Evolution—an unpublished Essay written several years before the appearance of the 'Origin' (24 Nov. 1859), by Searles Valentine Wood, junior. By Professor E. B. Poulton.

PROFESSOR POULTON gave a brief account of a manuscript written by Searles Valentine Wood, junior, and found by Sir Sidney Harmer among his father's papers. A note by the author, dated 1866, states that the manuscript was written 'about 1848 or 1849', but this is a mistake, for the Assistant Secretary had detected the water-mark of 1850 on the paper, and works referred to by the author as 'recent', were published in 1852. The manuscript, which had been much altered with large parts erased and often reinstated, brought forward several convincing arguments in favour of organic evolution—arguments employed by Darwin in the 'Origin of Species' (1859) but not, so far as the speaker was aware, published before that date. The essential parts of the manuscript, eliminating much repetition, would, it was hoped, appear in the Society's publications at an early date.

SIR SIDNEY HARMER expressed his satisfaction that Professor Poulton had completed the arduous task of editing this interesting manuscript. As bearing on its authenticity, he explained that his father, F. W. Harmer, a well-known East Anglian Geologist, had been an intimate friend of Searles V. Wood, father and son, particularly of the latter, on whose death the scientific MSS. of both passed into his possession. These consisted mainly of Geological notes, maps and drawings; and this part of the collection had been sent to the Geological Survey Office. The manuscript referring to organic evolution was obviously of very special biological interest, and it had accordingly been offered to, and accepted by, the Linnean Society. Until he read it, after his father's death in 1923, Sir Sidney had no knowledge of its existence.

MR. J. T. CUNNINGHAM also spoke.

THE PRESIDENT thanked Prof. Poulton for bringing this very interesting manuscript before the Society and for the trouble he had taken in extracting from it the essential points.

**The genus *Crocus* and its Cytology.
By Dr. E. J. Collins and Mr. K. Mather.**

DR. E. J. COLLINS spoke as follows:—

The genus *Crocus* has a remarkably long horticultural record. It is mentioned in classical writings, and it is known that five or six species were in cultivation in England at the end of the 16th century, almost 300 years before Maw's

'Monograph of the Genus' was published. These species were most probably *C. sativus*, *C. iridiflorus*, *C. aureus*, *C. vernus* and *C. versicolor*.

Attempts to classify the species were made by the following authors :—

1. HAWORTH. 1809. 'On the cultivation of Crocuses with a short account of the different species known at present.' Trans. Hort. Soc. Lond. vol. i, 1809.
2. SABINE. 1929. 'An account of the most remarkable varieties of spring Crocuses in the Gardens of the Society.' Trans. Hort. Soc. Lond. vol. vii, 1830.
3. HERBERT. 1847. 'History of the Species of Crocus.' Journ. Hort. Soc. Lond. vol. ii, 1847.
4. BAKER. 1873. 'Review of the known Species of Crocus.' Gard. Chronicle, 1873.
5. MAW. 1882. 'Notes on the life-History of a Crocus, and the classification and geographical distribution.' This paper was read before the Linnean Society on 19 January 1882, and is recorded in the Journ. Linn. Soc. vol. xix, 1882.
6. MAW. 1886. 'Monograph of the Genus *Crocus*.'

Haworth described thirteen forms and grouped them into two sections, the Piligeri, with bearded throats, and the Depilati, which are not bearded. Maw regarded this distinctive character as running in no way parallel with any other well-marked character in the species of the genus.

Sabine suggested a classification based upon the presence (Involucrati) or absence (Nudiflori) of a bract at the base of the scape, using the nature of the corm tunics, the possession of one or two bracts arising from the base of the ovary and the flowering period, for subsidiary grouping. Descriptions of species and garden varieties were intermingled; some six species and possibly a hundred vernal forms, chiefly of *C. vernus*, but including *C. versicolor* and some eighteen varieties of it, were recognized.

Dean Herbert described some forty-three species, including those set up by J. Gay 1827–31, and grouped them mainly on the characters put forward by Sabine, omitting, however, reference to the distinct annulate nature of the corm-tunic of some species.

Baker put forward a new basis of classification using the nature and degree of subdivision of the stigma, with subgroupings depending upon the colour of the flower and the flowering season. Maw rejected this basis, for community of character in the stigmata seemed to associate the species unnaturally; and there was a greater variety of type than could properly be represented by the three groups only, viz. Holostigma, Odontostigma and Schizostigma.

Maw cultivated Crocuses at Benthall Hall, Shropshire, and had a first-hand knowledge of the living plant. He himself, and in conjunction with Elwes, collected a considerable number of forms, and travellers and residents abroad by sending specimens enriched his collection of species, of which he grew some 68, and so he writes:—‘I have thus been enabled to grow in my garden almost the entire genus, to watch the life course of each species, and to make at my leisure the drawings of the plants, both in fruit and in flower, which have been produced in the coloured plates.’ It is not surprising that his Monograph provides an excellent account of the genus at the time of publication. The opening paragraph of Chapter II, however, makes it abundantly clear that the heterogeneity of the material presented many difficulties in identification and of interpretation, and he says of this:—‘In attempting a natural grouping and sequence of the species, a difficulty at once presents itself in the large number of well-marked characters possessed by individual species, which as it were interlace and overlap amongst the other species of the genus. . . . the tabular analysis shows that the concurrent grouping of several common characters is almost entirely absent excepting in very small and isolated sections; and it will be apparent that no one method of classification will enable the species to be arranged in strictly natural sequence or without making obvious gaps which some other method would more easily bridge over.’

He dealt fully with the geographical distribution of the species and drew attention to the variations which occur, but asserted that he had not been able to detect a wild hybrid *Crocus*, nor did he know of any authentic garden hybrids. There are now, however, many seedling forms with unknown pollen parent.

Within recent years a collection of *Crocus* species and varieties has been assembled at the John Innes Horticultural Institution, and preliminary cytological examination has shown that great diversity, both in the number of the chromosomes and the structure of the complex, exists in the group, and there seems little doubt that the difficulties of classification found in the morphological characters are envisaged in the internal nuclear constitution.

Mr. K. MATHER said that the series of somatic chromosome numbers shown by the genus *Crocus* is unusual, and must be the result of a comparatively complex type of evolutionary change.

Only a broad analysis of the various chromosome complements is possible, since individual chromosomes, which are recognized by their length, the position of their primary

(attachment) constrictions, and the number and position of their secondary constrictions, can be traced in a very few species.

The types of evolutionary change which may have gone on are limited. *Crocus vernus* provides some evidence for the occurrence of polyploidy, but there are no further indications of it, nor can it have given rise to such a series of numbers.

The production of forms with secondarily balanced chromosome complements, by hybridization between two unequal members of a polyploid series followed by inbreeding, would account for the series of numbers, but there is no direct evidence of this type of evolution.

There is, however, a certain amount of evidence, based on measurements of the chromosome complements of various species, for the occurrence of fragmentation and fusion of the chromosomes. These two processes are not simple, as has been assumed by earlier workers, but the asexual propagation of *Crocus* could allow of their occurrence.

Although *Crocus* and *Crepis* show similar series of chromosome numbers, it is probable that *Crepis* evolved by the achievement of secondary balance, since the order of size of the chromosomes is the same for all the species, unlike *Crocus* where the size of the individual chromosomes decreases as the number increases.

This complex evolution of the various chromosome complements explains the unsatisfactory position of the genus from the taxonomic point of view.

Prof. E. W. MACBRIDE said that he had listened to the paper with great interest, for many of the cytological facts were new to him and he desired further information about them. What exactly did Mr. Mather mean by the spindle-fibre? In animal cytology one distinguished fibres connecting a chromosome with the terminal aster from fibres connecting the two halves of a dividing chromosome with each other. The former kind of fibre had been shown by Dr. Gray to be temporary gellifications of cytoplasm, but the latter kind were the optical expression of a more permanent semi-solid structure known briefly as 'the spindle'. It was to the lasting credit of Dr. Shearer that he was the first to prove this, by squeezing the living eggs of the worm *Dinophilus* and forcing the spindle out. Dr. Shearer showed that the spindle could be rolled about like a reel of cotton on the slide.

Referring to the remarks of Professor MacBride, Professor R. R. GATES stated that in 1931 he had come to the conclusion that the spindle in mitosis was a compound structure. This was based partly on the accounts of the meiotic divisions in various parasitic insects, including

Acroschismus, *Llaveia* and other genera, in which a spindle-shaped zone developed in the nucleus around each chromosome. These probably represent an anisotropic condition of the karyolymph. They are at first oriented in all directions, but later become arranged parallel in a sheaf to form the spindle. From such results it appeared that the unit of spindle structure is the chromosome and its 'spindle fibre,' the latter being attached to the chromosome from the beginning and being derived from the nuclear sap rather than the cytoplasm. Professor E. B. Wilson had since come to the same conclusion regarding the nature of the spindle, based on similar evidence. More recently, investigations of the cytology of certain Malvaceae in his (Prof. Gates's) Laboratory furnished evidence that in plants also the spindle is a compound structure.

The PRESIDENT asked whether in the ascending series of chromosome numbers, the authors were able to correlate them with simpler and more specialized structure of the species of *Crocus*. He would like to know whether the more widely distributed and, therefore, probably the older species had a smaller number of chromosomes than the species of more limited range.

Dr. E. N. MILES THOMAS said that, as it was obvious that speakers were alluding to different parts of the 'spindle' used in the general sense, it would seem desirable to retain for the present the distinction between mantle or traction fibres and the central spindle fibres proper.

Mr. MATHER, in reply, stated that the use of the term 'spindle fibre attachment' as a synonym of 'primary constriction' implies nothing with respect to the occurrence or otherwise of spindle fibres as concrete bodies.

It is not possible to define the cytologically primitive form of *Crocus*, since, while we can distinguish theoretically between fragmentation and fusion of chromosomes, this cannot be done in practice, as the two processes are complementary.

Ranunculus Ficaria Linn.

By Mr. E. M. Marsden-Jones.

RANUNCULUS FICARIA is very widely distributed in Britain, occurring in all the vice-counties. It is to be found in two forms, one with bulbils in the axils of the leaves and one without. The distribution of the former is not yet known. L. N. H. Larter examined samples of both forms and found that the somatic chromosome number in the non-bulbil-producing plants is $2n=16$, diploid, and in the bulbil-producing $2n=32$, tetraploid. A distinction must be made between the two forms, as they differ considerably in several points, in three fundamentally, namely, the production of

bulbils in the axils of the leaves, vegetative reproduction and the number of chromosomes. It is suggested that plants that produce bulbils in the axils of the leaves be called *R. Ficaria* var. *bulbifera*. *R. Ficaria* is usually hermaphrodite, but it may also be gyno-monoecious and trioecious. The male plants are characterized by having petaloid sepals without nectaries, the carpels abortive or absent. The colour of the flower is usually *lemon-chrome*. Pollen and nectar are accessible to short-lipped insects; cross-pollination is essential as there is great self-sterility.

A germination test was carried out, and 71 per cent. of seed from non-bulbil-producing plants germinated; there was no germination from the apparently viable seed obtained from var. *bulbifera*. Before bulbil-formation is at its maximum seed appears to be forming normally, but when the maximum of bulbil production is reached deterioration sets in.

The conclusion arrived at is that the nutriment required for the formation of endosperm is diverted to the production of bulbils, and that under natural conditions no viable seed is produced.

A test made to determine the viability of bulbils produced in the axils of the leaves gave a growth of 81 per cent. Seed-counts from five non-bulbil-producing plants, growing in sun and shade, showed that the five sun plants produced 33 per cent. more viable seed than the five plants in the shade. The difference is not so great as might have been expected, and is accounted for by the fact that insects visit shade plants fairly frequently.

Thirty-five observations were made, lasting for twenty-six hours and fifteen minutes, between 15 March and 29 May 1931, to determine what insects visit *R. Ficaria*. The frequency and object of the visits were also recorded. A list of forty-eight species was obtained, comprising Coleoptera, Hymenoptera, Lepidoptera and Diptera. The conclusion arrived at from these observations is that *R. Ficaria* is adequately visited by insects under suitable weather conditions.

The research on which this paper is based has been aided by a Royal Society Government Grant.

Mr. I. H. BURKILL exhibited a plant in fruit obtained that day at Leatherhead. He said that fruits are easy to find in Surrey, which had seemed to him a climatic phenomenon, as they appear to be rare in the north of England; and there are other plants such as the Primrose whose fruits are much more difficult to find in the north than in the south: but that, if Mr. Marsden Jones's observation on the number of the chromosomes holds good, an entirely different complexion is put upon the question of fertility and its absence.

Professor R. R. GATES remarked that Mr. Marsden-Jones had described an extremely interesting case of tetraploidy. Although there was now no near species with which *Ranunculus Ficaria* could cross, yet he found it difficult to believe that the tetraploid form with bulbils and numerous other differences from the diploid had arisen simply as an autotetraploid through doubling of the chromosomes. It seemed to him, on the whole, more likely that the bulbiferous character and certain other differences had come in through an ancestral cross between diploid species, followed by chromosome doubling in the hybrid (allotetraploidy). Further investigation might throw light on this question.

The PRESIDENT expressed his interest in Mr. Marsden-Jones's communication. He thought that possibly the bulbil-producing form might be more common in the north, where the pollination of the flowers in the early months of the year might be more precarious owing to scarcity of insect life. At any rate, he was familiar with the bulbil-producing form in Lancashire and Cheshire.

Sir ARTHUR W. HILL referred to the fact that he had been successful in raising viable seed of the bulb-forming variety of *Ranunculus Ficaria* at Cambridge in the year 1905-6. This was done by cutting off the flower-stalks near the ground-level and placing them in water, and then removing the bulbils as they appeared in the axils of the leaves on the flower-stems. Several seeds germinated successfully.

The experiment has been repeated this year with Kew material of the bulb-forming variety, and seeds which appear to be viable are now ripening. The experiments seem to show that, unless the bulbs are removed, seeds are not formed on the bulb-producing variety.

Miss A. C. HALKET said that she was very interested in the paper, more particularly because a few years ago she did some experimental work on *Ranunculus Ficaria*. At that time she was especially interested in the reproductive structures, which, though generally called bulbils, are really small axillary buds bearing a swollen adventitious root or roots. Plants bearing these tubercles produce few fruits compared with the number borne by non-tubercle-bearing plants. However, if looked for at the right season, a few achenes can generally be found on tubercle-bearing plants growing in districts round London; and if these achenes are sown when mature they produce normal seedlings. Germination experiments with these fruits of *Ranunculus Ficaria* are difficult, as they often take a long time to germinate. The time usually is stated to be two years, and in her experiments though some germinated the first season others did not do so until the second year. The dormancy is apparently caused

by the hard pericarp that encloses the seed, for when the fruit-walls are removed, and the seeds grown under aseptic conditions, germination takes place readily. The rate of growth shown by the plants grown from tubercles in Mr. Marsdon-Jones's experiments is surprising. The rate of growth of *Ranunculus Ficaria* must be greatly influenced by the soil and other external conditions, for the plants grown from tubercles in pans in Regent's Park remained quite small for some years and did not flower.

11 MAY 1933

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 27 April 1933, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

A certificate of recommendation of the following candidate for Fellowship was read :—For the second time, in favour of Violet Margaret Grubb.

The following candidates were balloted for and elected Fellows :—William John Cooper Lawrence, Frederick Henry Reynolds, M.A., Ch.B., Puthenparampil Joseph Gregory, M.A., Doris Richardson, B.Sc., and William Stephenson.

The following candidates were balloted for and elected Foreign Members :—Dr. Elmer Drew Merrill, Dr. Erwin Baur, Professor Adolf Pascher, and Professor Filippo Silvestri.

The following candidates were balloted for and elected Associates :—Frederick James Killington and Thomas Sheppard, M.Sc.

**The Scarlet Tulip of the Near East, *Tulipa oculis-solis*.
By Sir Daniel Hall, K.C.B., F.R.S.**

THE scarlet tulip of the Near East has been recognized since Clusius and Parkinson, but confusion exists as to the specific identity and nomenclature of the many forms which range from Persia to Asia Minor and Palestine, and as denizens extend along the Mediterranean into the south of France.

Collected material from Turkestan, various Persian localities, Syria, Palestine, Asia Minor, Cyprus and the south of France is grown at the John Innes Horticultural Institution, and the discussion is based upon the comparisons of the living material.

The critical feature of the group is the presence of a dense felt of fine wool over the bulb within the tunic. This wool is present in all the individuals of any local form, and sharply distinguishes the group from the Clusiana group with a tuft of hairs at the apex only of the bulb, and the morphologically similar Gesneriana group which possesses a few silky adpressed hairs within the tunic. All these groups belong to the *Leiostemones* without hairs upon the filaments.

The habit of growth is generally upright, with narrow basal and stem leaves, glaucous and carrying a few short hairs on the edge of the leaves; but some of the forms have broad basal leaves at ground-level. The bud is carried to full height in the green state and then opens to a cup-shaped perianth, variable in general aspect with the variations in relative length and breadth of the inner and outer segments. The typical colour is a brick-scarlet, ranging to crimson or a deep claret-colour, but always with a yellow mesophyll. Characteristic is the presence of a blotch at the base of each segment, black or olive in colour, and very variable in shape and extent. This blotch is generally margined with yellow, but the blotch is not invariably present even in individuals of the same local form, and occasionally individuals occur in which the blotch is only faintly stained with olive on a yellow ground. Filaments, anthers and pollen are deep purple or black, though the individuals with a yellow blotch have yellow filaments and pollen. The ovary is green, usually contracted to something approaching a style at the top, with an overlapping stigmatic surface. This surface usually is yellow, but generally carries some scarlet or crimson, very variable in extent from form to form and from individual to individual within the form.

On cytological examination three of the forms proved to be triploids—*T. praecox* Tenore, a very distinct form native in Asia Minor and a common denizen in Italy and the Mediterranean region of France; a horticulturally distinct form from Syria which has been described as *T. Boissieri*; and *T. lanata* from Bokhara, one of the largest of known tulips. Omitting these from consideration the other forms exhibit great variation in such diagnostic features as habit of growth, breadth of foliage and perianth segments, shape of blotch, presence or absence of the yellow margin, &c., &c., and in these respects so far approach one another in individual specimens that they may conveniently be merged in one Linnean species.

The differentiation of species among many Monocotyledons like tulips presents special difficulties, because their power of vegetative reproduction, often assisted by a marked stoloniferous habit, may result in the wide extension of a clone. The persistence of such clones, followed by seed production from essentially self-fertilized individuals, must delay the action of natural selection, which with an annual rapidly reduces the population to a common type. Thus local forms become established which are little more than clones, but which get described as species because the range of variation, genetic or environmental, is not seen in herbarium specimens, which are selected individuals from a variable population.

The question then follows of the name that should be attached to this broad species. The earliest name appears to be *T. oculis-solis*, given by St. Amans in 1804 to a very distinct form, presumably native in Asia Minor but a denizen only in Italy and southern France, which is clearly described by Parkinson (Paradisi &c. 1629). Lindley's name of *T. montana* (Bot. Reg. 1106, 1827), which has been very generally used for the forms from Palestine, appears from the plate and description to have been applied to a distinct species, since called *T. Wilsoniana*, though later Lindley attached it to a specimen, now in the Lindley herbarium at Cambridge, from Iraq which does belong to the group under consideration. Dr. Stapf's name of *T. cuspidata* has also been generally used and properly refers to a broad-leaved form received from several localities in northern Persia. *T. Hoogiana*, a very large species from Eastern Turkestan, appears to be constant from seed and sufficiently distinct morphologically to rank as a species. Many other names have been given to forms which are horticulturally distinct as long as they are grown as clones, but only breeding experiments can decide whether it is more than a matter of convenience to distinguish them as species.

The PRESIDENT, in thanking Sir Daniel Hall for his interesting communication, pointed out the importance of the work Sir Daniel had carried out in checking, by the cultivation of so many Mediterranean and oriental tulips, the descriptions of the systematists. It was a satisfactory conclusion to assume that by their vegetative reproduction special races had become established in different regions, and that they might be united in the single genus of which so exhaustive an account had been given by Sir Daniel.

Dr. O. STAPF discussed the general problem of species in tulips.

In his reply Sir DANIEL HALL agreed with Dr. Stapf that in the end the recognition of a species must be a matter of judgment based on the broad general aspect of the population in the field.

**Revision of the genus *Lucilia* R.-D. (Diptera
Calliphoridae). By Miss D. Aubertin.**

THE genus is easily recognized and is composed of metallic-coloured flies generally known as 'Blow-flies'. After examining types from various Museums, and material from all over the world, Miss Aubertin has come to the conclusion that twenty-seven species may be recognized; of these two have fairly well-defined varieties. Eighty-two names have been listed as synonyms.

One species, *L. sericata*, is world-wide in distribution, and is probably European in origin: a second species, *L. cuprina*, occurs all over the tropical and south temperate regions, but for some reason has not penetrated to the north temperate zone; this species is predominantly African. There is a group of species common to palæarctic and nearctic regions, and certain other species characteristic of either one or the other region. Another group of species ranges over the Oriental and Australian regions, and is found among the palæarctic forms in Japan and on the Chinese coast.

The North American species are easily recognizable, but forms occurring south of the Canal zone are very difficult to determine. One species is fairly well characterized and occurs all over the southern continent, and there are probably three or four other good species: one finds, however, that characters (e.g. chaetotaxy and shape of genitalia) which afford satisfactory diagnostic guides elsewhere, break down, and the four types grade into one another.

There are several slightly aberrant species for which various authors have erected subgenera and even genera: one of these species is found in Alaska, another in the Galapagos Islands, a third in Hawaii and a fourth in Africa. There are apparently two clearly defined segregates within the genus which might rank as subgenera, but these taxonomic divisions have not been used in this paper because there remain certain residual species which cannot be placed in a single subgenus, and which do not provide characters of sufficient value for the formation of several more subgenera.

All species in the genus breed mainly in decaying animal matter. A specialization of this habit has led two species, *L. sericata* and *L. cuprina*, to the blowing of wool. The damage done in England in this way is not very great, but in Africa and Australia it assumes gigantic proportions. The fly lays its eggs in soiled wool, the maggots feed on certain

products of the disintegrating wool, and then either make sores or burrow into those already present and feed on the flesh and discharges; the health of the sheep is greatly impaired and the wool is rendered useless.

In connection with the habit of feeding in sores, it is interesting to note that the maggots of *L. sericata* have been used in recent experiments for clearing the rotting flesh out of wounds; when the wound has been cleared out, it is in a healthy condition and is found to heal readily.

One species of the genus, *L. bufonivora*, is parasitic on Amphibia, and generally attacks toads. The species is palaearctic and has rather a patchy distribution, occurring presumably only where toads are abundant. The eggs are laid round the eyes and nostrils, the maggots bore through the skin and finally kill the toad. This species is very closely allied to *L. silvarum*, whose larvae are not parasitic—in fact, it has only recently been recognized as a good species. It has almost certainly been derived from *L. silvarum* at a comparatively recent date, and the two species form what Villeneuve has called an 'espèce-jointive'.

Lucilia caesar has been recorded in Europe as breeding in carrion, and in the United States as breeding in human excrement; it has been shown, however, that the American record referred to another species, *L. illustris*, and that *L. caesar* does not occur in the nearctic region.

Professor E. B. POULTON said that Miss Aubertin was to be congratulated on bringing order into a group containing so many familiar, yet imperfectly known, insects. It was work of a kind which was especially needed by naturalists, and he was sure that they would welcome it most warmly.

On the modification of the alimentary canal in abyssal Cephalopods. By Mr. G. C. Robson and Miss. B. Bidder.

MR. G. C. ROBSON and Miss A. Bidder gave an account of the digestive system in a rare abyssal Octopod. This form, a description of which constitutes part of a paper submitted to the Society, was obtained by the U.S.F.C. 'Albatross' off the coast of Peru in 2370 fathoms. Mr. Robson and Miss Bidder gave a general account of the modification of the digestive system in abyssal Cephalopods, in the course of which very remarkable changes have taken place. They discussed the alterations in feeding-habits and digestion, which are possibly associated with the structural changes. They next gave a detailed account of the digestive organs in *Meteledone*, and such analysis as was feasible of the contents of the gut, and commented on certain evidence that suggested that digestion was partly internal (unlike *Eledone*), and on the marked reduction of the absorptive

surface. They emphasized the possibility that regurgitation of the stomach-contents, such as often occurs at death, might have taken place. This would make it practically impossible to tell from the contents of the crop the precise condition in which the food was swallowed.

Mr. W. C. WORSDELL exhibited two examples of abnormal inflorescences of *Scilla nutans* (the 'Blue-bell'). One of these was found by Miss Jean Allport in a wood at Halstead, Kent, the other was from a plant grown for the last three years by Dr. Turrill at Kew, originally from Nuneaton. In both all the bracts and bracteoles have developed as foliage-leaves, the individual flowers have become pedicellate, and the flowers perhaps somewhat paler. This sport has been named by Dr. Druce 'var. *bracteata*'. Mr. Worsdell compared it with the normal inflorescence in the Uvulariaceae, and especially with *Walleria nutans*, in which also single, nodding, pedicellate flowers occur in the axils of linear foliage-leaves. This type of inflorescence is probably the primitive one for the Liliaceae; and, if so, the abnormal inflorescence of *Scilla nutans* may perhaps be regarded as a reversion to an older type.

A study of *Veronica* from the viewpoint of certain floral characters. By Miss E. R. Saunders.

THE genus *Veronica* (used here in its widest sense) exhibits a quite exceptional degree of variation in certain features of the perianth. It would also seem to be unique as regards the independent behaviour of calyx and corolla in respect of meristic variations.

It is generally accepted that the primitive form(s) from which the present-day species have been derived had a pentamerous calyx and corolla. This condition persists to-day in the small New Zealand section *Pygmaea* and in two tropical species from E. Africa (*V. keniensis* R. E. Fries and *V. aberdarica* R. E. Fries), but the bulk of existing forms are characterized by a tetramerous calyx and corolla owing to the disappearance of the fifth posterior sepal and the congenital fusion of the two postero-lateral petals. In the remaining species the perianth is heteromerous. A group in the section *Chamaedrys* and individual species scattered among the other sections exhibit the combination K5C4, while two East African species (*V. linnaeoides* R. E. Fries and *V. Battiscombei* R. E. Fries) have typically K4C5 flowers. Pleiomerous corollas of 6, 7, 8, 9 or even 10 segments and oligomerous corollas of 3 or even 2 segments also occur sporadically in different species. In order to gain an insight into the way in which these several meristic variations are brought

about it is necessary to follow the changes in the vascular scheme which accompany them.

The earliest information which we have on this subject is the observation of Duvau, made a little more than a century ago, that in some *Veronica* species the posterior corolla segment has characteristically two main veins, whereas in others it has, like the anterior and lateral petals, only one. These two conditions we may conveniently indicate by the terms duplex and simplex. A microscopic examination of the flowers of different species reveals (a) that the two midrib bundles of the duplex posterior corolla segment arise on different radii, these radii corresponding to the positions proper to two postero-lateral petals; (b) that (so far as appears) K5C4 flowers always have a duplex posterior corolla segment; (c) that K4C4 flowers are of two kinds, some having a duplex, and others a simplex posterior corolla segment; (d) that C4 flowers of the duplex type exhibit a series of well-defined stages in vascular development grading down to the simplex condition as follows:—

- i. Duplex. (α) Two midribs, both branched bilaterally, the two systems remaining distinct throughout.
 - (β) Two midribs, both branched bilaterally, the two systems becoming continuous.
 - (γ) Two midribs, one branched bilaterally, the other unilaterally, the two systems remaining distinct. This grade appears in two patterns ('rights' and 'lefts').
 - (δ) Two midribs both branched unilaterally, the two systems remaining distinct.
- ii. Simplex. One midrib branched bilaterally.

It follows from the above (1) that the superposition of the posterior corolla segment on the posterior sepal, which is seen in K5C4 flowers, is an apparent, but not a real, exception to the law of alternation, since the segment appears to be always duplex; (2) that there are five types of normal flowers. These may be shortly indicated thus: K5C5m5*, K4C5m5, K5C4m5, K4C4m5, K4C4m4. The K5C4m4 combination, which would involve real superposition, was not observed and probably does not occur.

The C4m4 condition is characteristic of many (? all) species of the section *Pseudolysimachia* and of scattered species in other sections. These species, as a rule, are markedly stable.

All C4m5 species, on the other hand, exhibit some, and often considerable, variation in vascular development in the

* m=midrib.

posterior corolla segment, and many show occasional partial or complete reversion to C5. When such reversion is partial some degree of maladjustment not infrequently occurs between the processes of segmentation and vascular development, a branch from the vascular system of the one back segment traversing the boundary in the region where the two segments are conjoined and terminating in the other segment. Pleiomerous corollas with more than five segments (unconformable pleiometry) are produced in a different way from revisionary corollas (conformable pleiometry). In reversion each of the five petal midribs issues from the central cylinder separately and on a radius proper to a petal. When six or more petals are present the normal scheme of development, so to speak, 'goes wrong'. In the normal flowers of almost all *Veronica* species the sepals have marginal veins which are commissural in origin, the adjacent veins of two neighbouring sepals leaving the central cylinder conjoined with each other and with the petal midrib bundle of that radius, and later becoming disjoined from the petal bundle and from each other. In unconformable pleiometry the petal as well as the sepal component of these trunk-cords becomes involved in the process of bifurcation, two petal bundles being thus formed instead of one. Duplication of the petal accompanies duplication of the bundle, segmentation taking place in accord with this departure from the normal vascular scheme. Oligomerous corollas are usually due to suppression, more rarely to fusion.

The present observations reveal that the complete series of steps can be traced in the process of reduction from the primitive K5C5m5 form to the stable K4C4m4 *Veronica* types of to-day. They further indicate that this process of reduction is still in progress, and that the great majority of existing species are in an unstable condition as regards the particular floral characters involved.

Dr. T. A. SPRAGUE made some remarks, and Miss Saunders replied.

24 MAY 1933

ANNIVERSARY MEETING

Professor F. E. WEISS, F.R.S., President,
in the Chair

The Proceedings of the previous meeting, held on Thursday 11 May 1933, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—Puthenparampil Joseph Gregory.

The Treasurer presented his Financial Report and the Accounts of the Society, duly audited, for the year 1932–33. On a motion by Prof. Dame Helen Gwynne-Vaughan, seconded by Dr. Philippa C. Esdaile, the Report and Statement of Accounts were adopted.

The Bye-Laws regulating the Election of Council and Officers having been read by the Assistant Secretary, the PRESIDENT declared the Ballot for Council and Officers to be open, and voting began. The Ballot for Council was closed at 5.30 p.m. and for Officers at 6.0 p.m.

Meanwhile the Librarian and Assistant-Secretary presented his Report as follows :—

LIST OF THE SOCIETY.—Since the last Anniversary Meeting the Society has lost forty members. The detailed statement is as follows :—

16 Fellows by death :—Spencer Henry Bickham, Gilbert Charles Bourne, William Francis, James Groves, Malcolm Laurie, Frederick William Lucas, John Mastin, Edward William Alfred Augustine Mayhew, Sir Daniel Morris, Thomas Parkin, Arthur Rufus Sanderson, Basil Harrington Soulsby, John Stephenson, Leonard Goodhart Sutton, Mudumalakurti K. Venkata Rau, James Walter White.

2 Associates by death :—Herbert Clifton Chadwick, Andrew Scott.

4 Foreign Members by death :—Carl Erich Correns, Karl Ritter Eberhard von Goebel, Johannes Schmidt, Roland Thaxter.

15 Fellows by Withdrawal :—Sir Peter Henry Clutterbuck, Euan Hillhouse Methven Cox, Joseph Thomas Cunningham, Donald Ward Cutler, Frederick Eyles, George Herbert Fowler, Harold Kendall Hewison, Linnaeus Eden Hope, Roland Oscar Iliffe, Augustus Daniel Imms, Hugh Vandevaes Lely, John Frederick Marshall, Arthur Edward Osmaston, William Small, Raymond Henry Stoughton.

3 Fellows by Removal:—Amin Fikry, Frederick George Spring, William Robert Worthington Williams.

During the Session 4 Foreign Members, 2 Associates and 25 Fellows have been elected. Of the 25 Fellows elected, 22 have qualified. Also 6 Fellows have qualified who were elected at the end of last Session.

The present number on the List of Fellows is 750, with 4 Fellows elected but not yet qualified.

LIBRARY.—Between 1 May 1932 and 30 April 1933 15 works have been purchased and 528 books and reprints presented. (Special mention should be made of a generous donation from the Carnegie Institution of Washington of 86 volumes of its publications.) During the same period the number of volumes bound was 220; the number of volumes borrowed by Fellows and Associates was 1179, and by the National Central Library, 256. On the other hand, 11 volumes were borrowed from the Science Library for the use of Fellows. 1041 signatures were recorded in the Library Visitors' book, exclusive of 92 for Saturday afternoons.

LINNEAN COLLECTIONS.—Between 24 May 1932 and the 23 May 1933 the Herbarium has been consulted thirty-three times by visitors, who have examined one hundred and seventeen genera; the zoological collections have been consulted three times. Mr. J. R. Norman, F.L.S., has rearranged the Fishes and numbered the specimens in accordance with Dr. Albert Günther's catalogue.

At the conclusion of the Assistant-Secretary's report, the PRESIDENT appointed Mr. I. H. Burkill, Mr. H. W. Pugsley and Mr. A. W. Sheppard as Scrutineers of the Ballot.

In handing the Linnean Gold Medal to His Excellency the Swiss Minister (Monsieur C. R. PARAVICINI) on behalf of Professor ROBERT CHODAT, F.M.L.S., whose health did not allow him to be present, the PRESIDENT addressed him in the following words:—

In the present state of specialization it is not easy to be an expert in more than one or two of the many subdivisions of botanical science. In awarding the Linnean Medal to Professor Robert Chodat, F.M.L.S., the Linnean Society has selected a botanist, who like very few others may be considered a master in most branches of Botany. Systematists admire his careful work on the Polygalaceae and their geographical distribution, Ecologists have read with interest and profit his accounts of the Vegetation of Paraguay explored by him in 1914 and of Portugal, Spain and Majorca visited by him with his students.

In his laboratory at Geneva he has elaborated and perfected methods of obtaining pure cultures of Algae, methods which he has generously communicated to numerous Algologists. His own publications in Algology, culminating in his book on the Polymorphism of the Algae, have made him a recognized authority on the subject. More recently he has taken up the study of Fungi, more particularly the organisms of fermentation, and his sound knowledge of Chemistry and Physiology have enabled him to advance considerably our knowledge of fermentative processes.

It is important to note that it has not been with the minutiae of a subject so much as the broad principles that Chodat concerned himself, as is seen in his critical study of the palaeozoic Pteropsida and in his address on the conception of Species in Modern Botany. His contributions to the study of genetics if not numerous have been fundamental. Indeed, all fields of botany in which he has laboured he has enriched by his unremitting toil.

It is only natural that a man of such learning and distinction should have been a successful teacher, encouraging and stimulating his students by his own example. His admirable 'Principes de botanique' is at once a sound textbook and reveals at the same time his wide and philosophic outlook on botany.

Geneva has always been known for the pre-eminence of its botanical work, Robert Chodat has been a worthy successor of de Saussure and the de Candolles, and has continued the great traditions of botanical research. Nor has he limited his work to Geneva, but he has carried on his teaching and researches during the vacations at the alpine garden and laboratory, La Linnaea at Bourg St. Pierre, where many British students have come under his stimulating influence.

We had confidently hoped to welcome him among us this afternoon, but, alas! his medical officer will not permit him to undertake the fatigues of the journey. In handing to you, Sir, as representing Professor Chodat, the Linnean Medal, the highest distinction in our power to confer, I would ask you to be good enough to transmit it to him, together with our fervent hope that he may soon recover his normal health and strength to continue the important researches with which he is still occupied for the furtherance of botanical science of which he is a distinguished ornament.

In reply, Monsieur PARAVICINI expressed his profound appreciation of the honour that had been conferred upon his compatriot.

In the introductory passage to his Address, the PRESIDENT made the following statements :—

The past Session commenced with an interesting celebration of the centenary of the birth of our former Foreign Member Professor Julius Sachs. We had the pleasure of the presence at the meeting of two of his distinguished pupils, Dr. D. H. Scott and Professor F. O. Bower, who gave appreciatory addresses, and Professor S. H. Vines, a former President of the Society, also sent a valuable statement of Sachs and his work. The portrait of Sachs painted by his artist daughter, purchased by a number of Fellows, was presented to the Society, and now hangs in one of the anterooms.

The Council sent a congratulatory letter to Professor Max Weber on the occasion of his eightieth birthday. The Society was represented at Centenary Meetings of the Entomological Society of London by Dr. Hugh Scott, who also represented the Society at the Centenary of the French Entomological Society. Dr. A. B. Rendle was appointed by the Council to represent the Society on the occasion of the laying of the foundation stone of the new buildings of the University of London by His Majesty the King.

As reported by the Assistant Secretary the Society has lost a number of its Fellows by death, one of them, Sir Daniel Morris, a Fellow of 50 years' standing. I must, however, make special mention of the great loss we sustained by the death of Lt.-Col. John Stephenson, our Zoological Secretary. He was not only a zealous and efficient officer of the Society, but had endeared himself to all his colleagues by his sympathetic personal qualities.

Of the Foreign Members who have died Ritter von Goebel had shown particular interest in the purchase of Sachs' portrait by Fellows of the Society, and Professor Correns, though only elected a year ago, took an active interest in the Society's proceedings, which he showed by personal comments on matters raised at one of our meetings.

The PRESIDENT then delivered his Address on ' Variegated Foliage '.

On its conclusion, Dr. D. H. SCOTT, F.R.S., moved ' That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows '. The motion was seconded by Dr. A. B. RENDLE, F.R.S., and being put to the Meeting was carried with acclamation.

The Scrutineers of the Ballot, who had retired at the appointed times with the voting lists for the election of the

Council and of the Officers, having completed their scrutiny, reported to the President, and he declared the result as follows :—

COUNCIL FOR 1933-34.—Dr. W. T. Calman, F.R.S.; Prof. G. D. Hale Carpenter, M.B.E.; Dr. G. S. Carter; Dr. S. E. Chandler; Mr. Francis Druce; Professor J. Stanley Gardiner, F.R.S.; Professor H. S. Holden; Mr. H. A. Hyde; Professor W. Neilson Jones; Dr. Stanley Wells Kemp, F.R.S.; Mr. N. B. Kinnear; Dr. Margery Knight; Professor E. W. MacBride, F.R.S.; The Hon. Henry D. McLaren, C.B.E.; Mr. John Ramsbottom, O.B.E.; Dr. Hugh Scott; Dr. H. Hamshaw Thomas, M.B.E.; Miss E. M. Wakefield; Professor F. E. Weiss, F.R.S.; Mr. A. J. Wilmott.

(The retiring Councillors were Dr. Phillippa C. Esdaile, Professor T. G. Hill, Mr. G. W. E. Loder, Professor J. R. Matthews and Mr. J. R. Norman.)

OFFICERS FOR 1933-34.—*President*: Professor Frederick Ernest Weiss, F.R.S.; *Treasurer*: Mr. Francis Druce; *Botanical Secretary*: Mr. John Ramsbottom, O.B.E.; *Zoological Secretary*: Dr. Stanley Wells Kemp, F.R.S.

The PRESIDENT announced that he had appointed the following as VICE-PRESIDENTS for 1933-34.—Dr. W. T. Calman, F.R.S., Mr. Francis Druce, Professor E. W. MacBride, F.R.S., and The Hon. Henry D. McLaren, C.B.E.

The PRESIDENT then declared the Session of 1932-33 closed.

PRESIDENTIAL ADDRESS

By PROFESSOR F. E. WEISS, D.Sc., F.R.S., P.L.S.

VARIEGATED FOLIAGE.

(With 4 Text-figures.)

As variegated foliage is of an ornamental character it must have attracted attention ever since the early days of horticulture. My own interest in the subject has arisen through my studies of grafting and graft hybrids. One of the earliest scientific observations on variegated foliage is contained in a passage of Blair's 'Botanick Essays' published in 1720, in which, in discussing (p. 383) the circulation of sap, he states that 'the inoculating of a strip'd Bud into a plain Stock and the Consequence that the Stripe of Variegation shall be seen in a few Years after, over all the Shrub above and below the Graft is a full Demonstration of the Circulation of the Sap.' Blair's reference is to graftings made by Fairchild with a variegated form of the Jessamine. It was, however, not until the end of the next century that this interesting phenomenon of the transmission of variegation by grafting was seriously studied.

This was made possible by the discovery of a new and interesting case of variegated foliage. In 1868 there appeared in a collection of West Indian Plants, imported by Messrs. Veitch and Son, a specimen of *Abutilon striatum*, which, instead of the usual green foliage, had leaves showing a well-marked mosaic of green and yellow colour. Being a new and decorative form, it was propagated vegetatively and put on the market as *Abutilon Thompsoni*. M. Lemoine of Nancy, obtaining some of this material and wishing to multiply it by grafting, found that it caused the stock of *A. vexillarium* 2 to 15 centimetres below the graft to become variegated, and this was subsequently confirmed by other growers. The old green leaves of the stock were in no wise altered, only the new leaves that were formed were affected and developed variegation.

Morren in Belgium repeated this experiment in 1869, and concluded that the variegated foliage of *Abutilon Thompsoni* was without doubt a manifestation of a diseased condition of the plant. Beijerinck many years later, examining the mosaic disease of the tobacco in which the leaves become to some extent variegated, attributed the disease to a 'contagium vivum fluidum,' and that is also the view generally held with regard to what is now called the infectious chlorosis of the Malvaceae. For it has been shown that it is not restricted to *Abutilon* but can be transmitted to other members

of the family of Malvaceae, such as the hollyhock, *Althaea rosea*. Some Malvaceae, however, like the Tree Mallow (*Lavatera arborea*) are quite unaffected, and even some varieties of *Abutilon* do not respond to the contagium vivum. Baur has shown that this is not due to any lack of penetration of the disease, for by grafting first an immune variety on *Abutilon Thompsoni* and then a susceptible form upon the immune form, the virus, as he called the causal substance of the disease, travels up through the immune portion and causes variegation of the upper susceptible graft. Though Baur calls the active principle which causes this variegation a virus, it differs in many respects from the numerous viruses which have been shown to be responsible for the mosaic and other diseases of the potato, tobacco, and numerous other plants. For in these latter cases the virus present in the cells can be extracted by filtering the sap of the crushed cells, and when injected into a healthy plant, or transmitted by leaf-puncturing insects into a new host-plant, communicates the disease to it. In the case of the infectious chlorosis of the Malvaceae the contagium is bound to the living cell, and it is only by grafting a living piece of tissue upon a new host-plant that it can be transmitted. Baur concludes, therefore, that the virus is not itself an organism but some highly complex organic substance. Though it permeates the infected plant it must be present in a somewhat restricted amount, and is continually being formed anew during normal plant metabolism in the light. For if plants are placed in the dark for a time, and all the variegated leaves are cut away, the new etiolated leaves which have been formed turn green, and not variegated, when the plant is again exposed to light. This morbid organic substance does not appear to reach the reproductive cells, for the infectious chlorosis is not handed on to the offspring through the seed. Only seedlings with pure green leaves are produced. One is faced, therefore, with a difficulty to account for the first origin of the disease, for it cannot in Nature be handed on to other individuals, since it cannot be carried from plant to plant by sucking insects, as is the case with the more usual forms of virus. For the infectious substance does not exist except in a living cell of the plant. It manifests itself in the cells of the leaf by the yellow colour of the plastids, which should normally be green. Evidently the peculiar morbid substance prohibits the formation of chlorophyll. But, if it does so, why are not all the cells of the leaf yellow? Are the green cells not penetrated by the virus or is their protoplasm more resistant to its action? We may probably assume that the green cells are permeated by the virus, since it has been shown that such Malvaceae as are unaffected by it can

conduct it through their tissues. There seems, therefore, still much to be learnt about its nature, as up to now we only know its manifestations.

As mentioned above a similar transmissible variegation through grafting was known as far back as 1720 in the case of the Jessamine, and more recently Baur has shown (1907) that the peculiarity of a variegated form of the Golden Privet (*Ligustrum vulgare foliis aureo-variegatis* of Späth) can be transmitted by grafting and is, like the chlorosis of the Malvaceae, dependent upon light. In this case also the seedlings have pure green leaves.

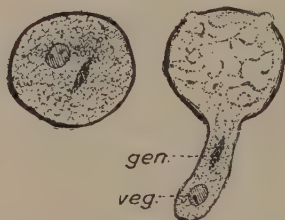
A similar chlorosis occurs in the *Laburnum* and, as it shows itself also in the bark, transplantation of pieces of the infected bark will induce on the so treated stock chlorosis of the leaves which subsequently arise. The *Laburnum* chlorosis can be transmitted by grafting to other species of *Cytisus* such as *Cytisus hirsutus*, but not to *Cytisus purpureus* or *C. alpinus*.

The Ash, *Fraxinus*, too, may be affected by a contagious chlorosis. Infectious Chlorosis is, therefore, a widespread phenomenon and possibly many other plants with variegated foliage may be found to be similarly affected. Whether the organic substance which induces it is the same for several or all of these plants cannot at present be determined, as it can be transmitted only by grafting, and a union of tissues can take place only between nearly allied plants.

Inability to form chlorophyll, which is characteristic of infectious chlorosis, is obviously a phenomenon which may be due to various causes. As I pointed out in the discussion on the mortality of young plants opened by Prof. Salisbury, it has been shown by experiments made at the Welsh Plant Breeding Station that the number of non-viable albino seedlings is considerably increased in the case of some self-fertilised grasses, and Jenkins has shown that in others seedlings deficient in various degrees in chlorophyll are also the result of inbreeding, which causes a lowered vitality in the offspring. It has also been shown that hybridisation in some cases gives rise to variegated plants. Thus Smith Langley records (J. R. H. S. 1915, p. xxxvi) that all seedlings produced by crossing *Pelargonium denticulatum* with *P. filicifolium* were variegated, while both parents were pure green. Species hybrids, in which *Pelargonium citriodorum* was one of the parents, produced variegated offspring, but only in the second filial generation. Perhaps one must assume some incompatibility of the living substance, nucleus or protoplasm, of the two parents or some upsetting of the equilibrium as the cause of the inability to produce a normal green colour. Renner, experimenting

with *Oenothera*, has shown that many reciprocal hybrids differ in the colour of their foliage. Some are green, others pale green or albinos, which, of course, do not arrive at maturity. Others may have variegated leaves and may become later pure green or pure pale or definite chimeras, i.e. show an orderly segregation into pale and green sectors. He explains these varying conditions of greenness by assuming that some of the plastids may belong to the female parent and were present, at all events, in embryo in the egg-cell, while other of the plastids may have come over from the male parent together with the male fertilising nucleus. These paternal plastids were possibly unable to become green in the strange cytoplasm of the egg-cell, or possibly the presence of the heterozygous nucleus exerted some inhibition. The passage of minute plastids, the forerunners of the chlorophyll grains through the pollen-tube from the male parent to

TEXT-FIG. 1.



Pollen-grains of *Lupinus*, after Ruhland and Wetzel.

The pollen-grain on the right has germinated.

gen.=generative nucleus surrounded by plastids.

veg.=vegetative nucleus concerned in growth of pollen-tube.

the egg-cell of the female parent, may have seemed fanciful a few years ago, but since Ruhland and Wetzel (1929) have shown that such plastids are closely associated with the male nucleus in the pollen-grain and the pollen-tube of the *Lupin*, it is obviously possible that in other plants too the fertilised egg-cell may contain plastids derived from both parents. This observation of the transference of plastids from the male to the female parent has raised acutely the question to what extent the cytoplasm, as well as the nuclei of the two parents, may be concerned in the process of fertilisation, and botanical geneticists like Baur, Correns, Renner, and Winkler are inclined to attribute considerable importance in inheritance to the influence of the cytoplasm in addition to the fusion of nuclei in the process of fertilisation.

While in the higher plants the influence of the 'plasmon,' as it has been called, is based on theoretical considerations resulting from breeding experiments, Harder has demonstrated (Zeitschrift. f. Bot. 1927), by delicate microsurgical experiments on hymenomycetous fungi, that in cell-fusions the cytoplasm in the absence of the corresponding nucleus may determine the development of certain specific characters,

Experimenting with a variegated form of the Marvel of Peru (*Mirabilis Jalapa albomaculata*) Correns has shown that by self-pollinating this plant green, white, and variegated offspring are obtained, no doubt due to the particular colour of the tissues in which reproductive cells have arisen. If, on the other hand, the variegated plant is crossed with pollen of a normal green plant of this species or vice versa, variegation or greenness are inherited only through the female parent. He concludes, therefore, that in this case no protoplasm passes over with the male nucleus into the egg-cell.

The variegated form of the Snapdragon (*Antirrhinum majus albomaculata*) described by Baur agrees entirely in its behaviour with the variegated *Mirabilis*. Its variegation is inherited only through the female plant. So is variegation in *Primula sinensis* according to Gregory. Here too the offspring obtained by selfing are green, white, or variegated. On the other hand, the variegated Hop, *Humulus*, described by Winge, though transmitting its characteristic foliage only through the female parent, does not produce green and white as well as variegated offspring but only the latter.

The *Capsicum* described by Ikeno, like *Humulus*, also produces only variegated offspring, but this character is transmitted both through the female and the male parent. Lastly, we have a fourth category that is represented by the garden Geranium (*Pelargonium zonale*), in which both parents transmit variegation, but in which like *Mirabilis* and *Antirrhinum* green, white, and variegated offspring occur. Winge accordingly classified inheritance of variegation into four types represented by the examples just named. As since 1919 other forms of variegation have been studied in detail Scherz* has further elaborated Winge's system classifying variegation into :

- I, forms in which the nucleus contains the factors for variegation (*Mirabilis*, *Antirrhinum*, and *Primula*).
- II, forms in which the cytoplasm determines variegation (*Capsicum* and *Humulus*).

* Scherz, W., "Beiträge zur Genetik der Buntblättrigkeit," Zeit. f. induct. Abstamm. vol. xlv, 1927, p. 1.

III, forms in which the plastids themselves determine variegation, and in which plastids as well as protoplasm pass over from the pollen-grain into the egg-cell. This category contains the variegated *Oenotheras* referred to previously as well as *Geranium*, *Erodium* and *Pelargonium*.

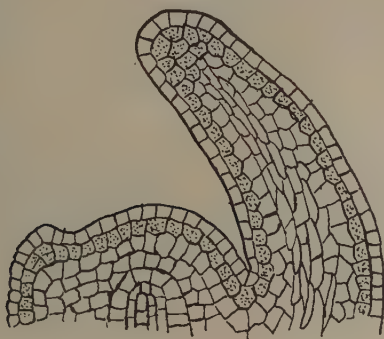
Scherz's classification is very complete and more elaborate than my summary of it, and should certainly be consulted by all who are interested in the question of inheritance of variegation.

It may be of interest to give as a concrete example of inheritance of variegation an account of the behaviour of *Pelargonium* so carefully worked out by Baur. This is a plant in which variegation is transmitted by both parents, so that we must assume the transference of plastids accompanying the male generative nucleus.

It is common occurrence in variegated plants to find some branches which are entirely devoid of green colour, having been developed from a complex of chlorotic cells. Plants destitute in this way of the food forming green colouring-matter could not lead an independent existence, and such a white branch leads as it were a parasitic existence, drawing its food-material from those portions of the plant which contain chlorophyll. Thus nourished such an albino branch can form flowers, and if one uses its pollen one is practically using a non-green male parent. If the flower of a green plant is pollinated with such pollen, the result is a series of offspring which are particoloured, showing in the seed-leaves already patches of green and patches of white tissue. We may speak of this as a mosaic inheritance of the two parental characteristics. These are not blended together in each of the cells of the offspring, nor is one of them dominant over the other as is the case in Mendelian inheritance, but irregular patches of tissue are either pure green or pure white. In such variegated seedlings of *Pelargonium* the segregation into green and white cells is strikingly apparent. If a green patch occupies the small growing point of the main shoot the plant will grow up entirely green. If a white patch is at the apex of the shoot the developing stem will have only white leaves and the plant dies for lack of nutrition. If the apex is particoloured, the shoot will bear both green and white leaves, and some that arise at the juncture of green and white tissues will be green and white in varying degrees. We thus obtain what is called a sectorial chimera. It may also happen that on the side of the stem, if the white tissue overlies in form of a thin strip, an underlying green centre, a shoot may arise with a skin of white cells one or two layers in thickness surrounding a central green core. In such cases

the edge of the leaf, the tissues of which arise largely from the two outermost layers of the shoot-tip, will be white, while in the central portion of the leaf the underlying green cells of the leaf will be visible through the transparent white cells. Such forms have been termed by horticulturists albo-marginatae. Botanically they have been termed by Baur periclinal chimeras. They exist in many groups of plants, though their mode of origin is not always known. But, since Baur has shown experimentally how they arise in *Pelargonium*, we may infer that they have often arisen in a similar manner in other plants.

TEXT-FIG. 2.



Young developing leaf to the right of the stem-apex. It shows that a considerable amount of tissue at the leaf-tip is formed from the subepidermal layer of the stem-apex. The cells derived from this layer are dotted. If these cells belong to a colourless constituent the leaf will be white-margined, if to a green constituent the leaf will be green-margined.

A not uncommon feature of these white-margined varieties is that they produce reversions to a purely green type of leaf. We may assume that in such cases the underlying green tissue has pushed its way through to the surface, owing to some injury to, or defect in, the epidermis. Indeed, occasionally a leaf is produced in which one half is white-margined and the other half is green. The latter is generally larger than the white-margined half, as it is better nourished, since it contains a larger amount of chlorophyll. More rarely do we find reversions to purely white leaves which must be explained by abnormal multiplication of the cells of the white tissue to the exclusion of the green.

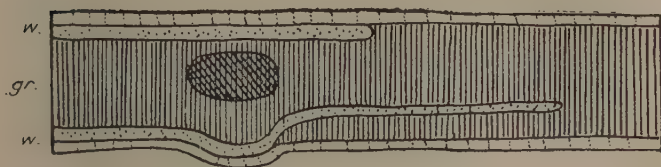
In the same way as we can explain the origin of the white-margined varieties, we must explain the much less common green-margined varieties. These are known only for comparatively few plants (*Coprosma*, *Vinca*, *Hydrangea*, *Euonymus*, and *Pelargonium*). In these cases the leaves are found to be covered by two layers of cells derived from the green skin and surrounding a white core. The outermost layer of cells is, of course, colourless. For even in normal green leaves the outermost layer of cells contains no chlorophyll except in the guard-cells of the stomata. Therefore, in these periclinal chimeras of the green over white type the green colour can only be seen in the subepidermal layer. But since in the development of the margin of the leaf the subepidermal cells by their multiplication play a considerable part, the margin of the leaf has a normal green colour; while near the centre of the leaf there is only a single layer of green cells overlying the white core. The leaf, therefore, is pale in the centre, but has a deep green border and may be termed green-margined. Leaves of this form of chimera are very variable in the amount of green they contain, considerable masses of green tissue often extending from the margin towards the centre. This must be due to irregularities in leaf-development, and more information is still required as to the part played by the various layers of cells in the development of the leaf. The stems of this type of chimera are generally pale, often nearly white owing to the central white core. In extreme cases, such as *Hydrangea* and the *Pelargonium*, known as Freak of Nature, the leaf-stalk, the stipules, and the centre of the leaf may be quite white, only the margin of the leaf being green. As in the case of the white-margined varieties of leaves, the condition in the green-margined form is unstable, and purely white or purely green leaves or branches may arise by either the breaking through of the white tissues or by proliferation of the green superficial cells.

A further peculiar feature, which was specially studied by the late Dr. Bateson, was the phenomenon of reversal observed in these periclinal chimeras, in which a white-margined variety changed into a green-margined variety. This has been described by him for *Euonymus japonica variegata*, *Pelargonium Madame Solleroy*, and *Coprosma Baueri variegata*. This phenomenon is rare and exceptional, and so far no definite explanation can be given of it. It is obviously not due to any injury but to some instability of constitution or development which is well worth further study. Miss Massey has described and figured the internal arrangement (fig. 3) of the tissues in the case of an incipient reversal in *Pelargonium elegans*, from which it would appear that the change from a white over green to the green over

white form was due to the inward growth of the white tissue, which thus becomes covered by green cells. The cause for such a change is still unknown. Once the green over white condition is established it seems to remain constant, and no reverting to the white over green has been observed.

The inheritance of the white and green margined varieties is of particular interest, as it emphasises the chimeral nature of these forms. Reproductive cells in the Flowering Plants are always formed from the subepidermal layer, and, since the explanation of the white and green margined varieties assumes that the constituent cells of the plant are in two distinct forms green and white, the offspring are either all white or all green according to the constitution of the subepidermal layer of cells. For the narrow white-margined forms, which have only a single layer of white cells around the green core, the seedlings are all pure green, but when

TEXT-FIG. 3.



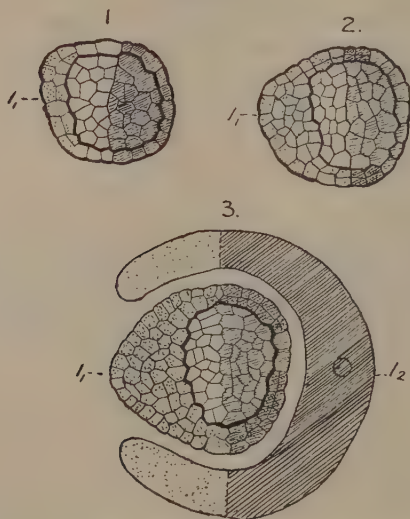
Section across reversed leaf of *Pelargonium elegans*, after K. Massey.

On the right of midrib the leaf is white-over-green; to the right of the midrib the white tissue has become submerged on the underside by green tissue.

we have two layers of the colourless cells covering the green core, the offspring are all albinos and as such not viable. In the green-margined varieties so far all the forms have a skin of two layers of green cells, hence the subepidermal layer is green and all the offspring are green. It is of interest to note that this same rule holds good for the graft hybrids *Cytisus Adami* and *Crataego-mespilus Asniersii*. In the former case a core of the Common Laburnum is covered in by a single layer of cells of *Cytisus purpureus*. On the rare occasions when *Cytisus Adami* forms fertile seeds, the latter give rise to pure Laburnum seedlings. In the graft hybrid between the hawthorn and the medlar *Crataego-mespilus Asniersii*, the core of the plant is formed by the hawthorn and the epidermis alone is derived from the medlar. Here, too, when viable seeds are formed, the seedlings are found to be pure hawthorns.

The plants so far dealt with in connection with white-margined varieties have been Dicotyledons. Monocotyledons must be dealt with separately, as there has been some doubt whether they can form periclinal chimeras. In some Monocotyledons, like the grasses, in which white-striped and green-striped varieties occur, these, though resembling in appearance the green over white and white over green chimeras met with in the Dicotyledons, have a different constitution. Rössler

TEXT-FIG. 4.



Three sections through the young leaf of a grass at various stages of development. The tissues of the stem are supposed to be sectorially white and green. The latter cells are shaded. As development of l_1 proceeds, the tissues of the leaf formed from the epidermis progress round the axis so as to partake at their edge of green tissues, while the centre of the leaf is white. This leaf (l_1) will, therefore, be green-margined, while the leaf below (l_2) will be white-margined, (adapted from Rössler).

has shown that in the wheat (*Triticum vulgare*) the leaves are formed entirely from epidermal cells of the stem apex, the tissues of the leaf are therefore all of one kind as far as their origin is concerned. Probably this is true of other grass leaves, including those with the green and white stripes. If we take as an example the leaf of a variegated *Dactylis*, we find that some of the leaves have a green centre and white margins, while others have a white centre and green margins

thus resembling the two types of periclinal chimaeras investigated by Bateson. But careful examination of the stem shows that the latter is a sectorial chimaera—half of the stem containing chlorophyll, while the other half is colourless. As the leaves arise in two rows each forming a complete sheath around the stem, those springing from the green side of the stem have a green centre and white margins, while those arising from the white portion of the stem will have green margins (see fig. 4). If the green and white tissues were geometrically differently arranged they would produce leaves which were half white and half green.

Dr. Collins has found that a similar explanation holds good for *Chlorophyton* (*Anthericum*) *elatum* and *C. comosum*, in which similar striped leaves occur. Here also the chlorotic areas of the leaf arise from a block of chlorotic tissue on the stem. This is borne out by the genetic investigations which Collins has carried out. The white-margined variety has green axillary inflorescences as they arise opposite the green centre of the leaf. Such green flowering shoots produce green seedlings only. In cases where the flowering shoot falls in a particoloured area the seedlings will be white, green, or variegated, according as the ovule with the egg-cells which it contains falls into a white, green, or particoloured region.

Still, though these narrow monocotyledonous leaves of *Dactylis* and *Anthericum* are of the nature of sectorial and not periclinal chimeras, it is possible that some of the wider-leaved Monocotyledons may form periclinal chimeras. We must remember, however, that in the origin of most monocotyledonous leaves only the two outermost layers of cells of the stem-apex take part, so that the periclinal chimera in Monocotyledons can have only a skin-covering of one layer of cells. As the epidermis of leaves is, however, always colourless, it might be difficult to determine whether the skin belonged to a white or green variety. Professor Chodat has, however, shown how this can be determined with certainty. For, though it is true that the epidermal cells are devoid of chlorophyll, this is not true of the guard-cells of the stomata, which in all ordinary green leaves contain chlorophyll-grains necessary for their opening and closing. It is this point which Professor Chodat seized upon to demonstrate that in *Funkia Sieboldiana* var. *medio-variegata*, which has a white centre to the leaf and green margins, the epidermis is of a green type, though all the epidermal cells with the exception of the guard-cells are colourless. On the other hand, in *Funkia Sieboldiana* var. *albo-marginata* even the guard-cells of the stomata are colourless, and the skin, therefore, would seem to be formed of albino tissue. It seems, therefore, definitely demonstrated that periclinal chimeras can and

are occasionally formed among Monocotyledons. In the case of *Funkia* we must assume that some of the subepidermal cells at the edge of the leaf have resulted from periclinal division of the epidermal layer of the stem apex, a not unusual occurrence. It would be useful to work out the leaf-development in this plant, and it would also be an interesting physiological experiment to investigate the functioning of the stomata in the case of leaves devoid of chlorophyll in their guard-cells.

More recently Yasui has described another variegated form of *Funkia* or *Hostia japonica albomarginata*, which was apparently not of chimeral nature, as one must gather both from the fact that some of its cells contained both green and white plastids and also from its genetical constitution. It is of interest that a similar appearance of the foliage may in the same genus be due to different constitutions.

I have said nothing so far about the occurrence of variegated leaves in Non-Flowering Plants. Several instances are known among the Pteridophyta. Schwarz has recorded the occurrence of colourless leaves on the fronds of *Selaginella Martensii*. Investigation of the plants has shown that this phenomenon is due to the influence of temperature. When grown at 10° C. or less colourless leaves appear, while if the temperature is kept above 10° C. only green leaves are formed. The latter contain normal green plastids, but in the colourless leaves one encounters cells with more or less degenerate and vacuolated plastids, and, finally, cells devoid of plastids. The variegation of this plant is, therefore, a physiological phenomenon and not a constitutional character, though it may be that this particular form is particularly sensitive to temperature, and reacts in this special way to low temperatures.

Variegation more akin to that occurring among Flowering Plants has been described for various species of ferns by Miss Andersson-Kottö. Variegation in this group of plants is of particular interest, since the life-history of the fern contains two independent generations, the fern-plant or sporophyte producing asexual spores on the back of the frond, giving rise to the minute prothallus, which reproduces sexually and produces the sporophyte. Moreover, these two generations of the fern are genetically distinct—the prothallus being haploid, the sporophyte diploid. Accordingly, it may be of interest to follow in some detail one of the cases investigated by Miss Andersson-Kottö. The first example described by her was that of a variegated fern frequently cultivated in botanic gardens, namely a form of *Adiantum cuneatum*, in which some of the pinnules may be pure white while the majority are green, but may be marked by white stripes

or wedge-shaped areas, due to the peculiar division of the wedge-shaped apical cell. Sporangia are borne both on the white and on the green areas, but the former are badly developed and do not give rise to viable spores. The spores produced on the green part of the frond give rise to prothalli of two types, pale green growths, which soon die, and dark green prothalli looking at first quite normal, but they soon produce white wedge-shaped areas, which have become so by a degeneration of the chlorophyll. The prothalli are, therefore, all variegated. The sporophytes to which they give rise are also all variegated. Sometimes these variegated sporophytes develop so much white tissue that they become albinos and die. On the other hand, if the first leaf was completely white the apical cell, which has produced this white leaf, may proceed to the production of further green leaves. It is obvious, therefore, that we have in the case of this fern a somatic segregation into green and non-green cells from the apical cell, both of the gametophyte and the sporophyte. We must assume that some factor for destruction of chlorophyll is liberated at cell-division.

The other ferns investigated by Miss Andersson-Kottö more recently are to some extent, but not completely, in agreement with the example just given. In a variegated variety of *Polystichum angulare* the spores also produce green, pale green, and variegated prothalli. The latter may give rise to true breeding green sporophytes and also to variegated fern-plants.

In *Lastrea atrata* var. *variegata*, spores both from green and white areas produce dark green prothalli indistinguishable from each other, both of which give rise to variegated sporophytes. Lastly, in a variegated *Scolopendrium* the spores give rise to both dark and pale green prothalli—the former producing green sporophytes, the latter variegated sporophytes.

The differences in behaviour of these various ferns may seem at first somewhat bewildering, but all these cases are of particular interest as they illustrate so clearly the somatic segregation into normal green cells, and others which seem to contain a factor for destruction of chlorophyll. Since the tissues of both the sporophyte and the gametophyte arise in ferns from a single apical cell, it, or its immediate derivatives, must possess this power of segregation.

From the foregoing account it might appear at first sight that the inheritance of variegated foliage is as varied as is the colour of the leaves, and followed no known laws. That is, however, not strictly correct. In the various cases of infectious chlorosis, due to some agent or virus, the latter does not affect the reproductive cells, and consequently all seedlings are pure green and breed true. Such variegated plants

must be propagated from cuttings or by grafting. Again, in all those white-margined varieties which are of the nature of periclinal chimeras, that is, in which a green core is covered in by white skin of one or two layers of cells, since the reproductive cells belong to the subepidermal layer, the seedlings are either pure green or pure white, green if the leaf is covered only by one white layer and white if the subepidermal layer also is derived from a white parent. In the less numerous cases of green over white periclinal chimeras the same holds true. In the white and green striped leaves, which are not periclinal chimeras, but in which there are median and marginal solid blocks of white and green cells, the offspring partake of the nature of the median block. A certain number of variegated leaves follow the Mendelian rules when crossed with green forms. The green colour is usually dominant, and the variegated form recessive. The factor for variegation must therefore have its seat in the nucleus. Among these forms many are mentioned albino forms of *Melandrium*, citrina forms of *Antirrhinum*, variegata forms of *Mirabilis*, and albomarginata forms of *Arabis*.

There are, however, as I have indicated, other cases of variegation which do not conform to the rules of inheritance formulated by Mendel. Many strict exponents of Mendelism have attempted, by the assumption of some inhibitory factor or factors in the nucleus, to bring these exceptional cases into harmony with the Mendelian rules. But the more general view, to which those who have occupied themselves with the inheritance of variegation have come, is that in many cases the protoplasm of the generative cells and even its inclusions, the plastids, play their part in determining inheritance. If this is true for variegation, we may, I think, assume that in other cases, too, where inhibitory factors have been assumed to be present in the nucleus, the inhibition may have its seat in the protoplasm or plasmon. The study of exceptional phenomena is often very useful, and it certainly causes us to revise many preconceived ideas. From that point of view the further investigation of variegation may be recommended both to the plant physiologist and the geneticist, for the fundamental problem why green and white plastids should occur so distinctly segregated in definite groups of cells has never been solved. They may arise, as we have seen in the case of the fern, from the same meristematic cell, from which green or white cells may be produced, and in the case of the Flowering Plants, seedlings with patches of green and white cells, owe all their tissues in their inception to the division of a single cell, the fertilized egg-cell. To what physiological or genetic causes must we

attribute the healthy green plastids of one cell or group of cells and the degenerate pale yellow or colourless plastids of another ?

Variegated leaves are only one example of somatic segregation of characters. It includes many characters of the floral organs, fruits, and the general phenomenon of bud-variation. As R. J. Chittenden says in his useful summary of Vegetative Segregation, 'Vegetative segregation is a term of very wide application and embraces a vast mass of unrelated phenomena which are anomalous and inconsistent to the general orderliness of behaviour.' No one can accuse the late Dr. Bateson, whose untimely death we of the Linnean Society particularly mourn, of want of appreciation of work along Mendelian lines. Yet after a fruitful life spent in testing and extending Mendel's laws he says in his Joseph Leidy Memorial Lecture on Segregation :—'Phenomena to which the simple chromosomal theory is inapplicable, save by the invocation of a train of subordinate hypotheses have been met with continually, as even our brief experience of some fifteen years has abundantly demonstrated. Through all this work, with ever-increasing certainty, the conviction has grown that the problem of heredity and variation is intimately connected with that of somatic differentiation, and that in an analysis of the interrelation of these two manifestations of cellular diversity lies the best prospect of success.'

In view of the stress Bateson lays upon the study of somatic differentiation, I hope that I may have been justified in bringing before you a subject which I trust you have not found to be devoid of interest, and which I believe is important as a field for further study and for the successful elucidation of the problem of variation and heredity.

THE HOOKER LECTURE

[Read 16 February 1933]

SOME ASPECTS OF THE BEARING OF CYTOLOGY ON TAXONOMY.

By PROFESSOR SIR WILLIAM WRIGHT SMITH, M.A.

I HAVE first to thank the Fellows of the Linnean Society for the honour they have done me in asking me to give the Hooker Lecture. I understand that one of the conditions is that the subject should be in some degree associated with the name and with the work of Sir Joseph Hooker. That ought not to be a difficult matter when one surveys the wide field represented in the publications of so distinguished a botanist. And so my first impulse was to turn to the record of his work as detailed year by year in the 'Kew Bulletin' of 1912. He began to publish in 1837, and did not lay his pen aside till the year of his death in 1911—74 years of devotion to his subject. As for the subject-matter, he appears to have left no part of the botanical field untouched from Lichens, Algae, Hepatics, and Mosses to the Angiosperms and Palaeontology. I have been told that in his latter years his chief regret was that he could not undertake more per day than six or seven hours of work which entailed the use of the microscope. After all, facile critics of the Victorian epoch are wrong—for there were giants in that day, and Hooker was among them.

Systematists are not able—as most scientific workers are—to restrict their attention in great part to the latest works on their subject. There is always the difficult problem of priority. The systematist in his description of new species raises for himself a monument more lasting than bronze, and, even if he makes mistakes in classification which would be most reprehensible in a junior student, his errors live after him, are duly recorded and annotated, and, though often transformed in appearance, are apparently immortal and will be quoted *ad infinitum*, even if relegated to the literature of synonyms. Consequently, the working systematist has to pass in review the oldest—as far as Linnaeus anyhow—as well as the newest work on his genus or species, and to evaluate the conclusions of his predecessors of even 100 years before. Thus, apart from their intrinsic merit, the solid contributions of Sir Joseph Hooker, such as his 'Flora of British India', the 'Flora of New Zealand', and so on, have a permanence which cannot be assailed and must remain as the foundation of future work in the areas concerned. To the

systematist dealing with the floras of countries within the confines of the British Empire no name comes more frequently to his view than that of Hooker.

I have had the pleasure of retraversing most of the ground which he has described in his classic Himalayan Journals and of seeing nearly all the plants which he discovered there. These wonderful Alps of Sikkim are still unspoilt, and you can go yet to Hooker's localities and find the scenes and the plants unchanged. I can bear testimony to his powers as a collector. Difficult as the country was in his day, the young Hooker left but few gleanings to his successors. Even in such a genus as *Rhododendron*, prolific in species, he left not one untouched—and they were duly adorned in his 'Rhododendrons of the Sikkim Himalaya'. For the last 60 years collectors have gone to that region, but no indubitable new species of the genus has rewarded their efforts. My acquaintance with one of his areas and my frequent consultation of his works and collections may perhaps serve as reasons for my venturing to accept the honour of giving this address.

In dealing with the floras of areas where Hooker was often-times the pioneer, one naturally comes to conclusions as to his methods and his points of view in the discrimination of species. His main publications followed the accepted lines of systematic botany. Nor did the advent of the 'Origin of Species', his close friendship with Darwin, their intimate debate, and correspondence on the many new problems of the Darwinian period appear to affect the broad general policy which he had already adopted in his work on the floras of various important areas. Systematists generally were uninfluenced and continued to be anchored to the 'Linnean', as is now its term. The period of experimental research and of fine subdivision had yet to come. Hooker had to deal with enormous collections and could do no other than he did. Consequently, his conception of what constitutes a species is a wide one—and from the point of view of a general flora an eminently practical one. Acquainted to an astonishing extent not only with the flora of the country under review, but also with the flora of the adjacent areas, he was attracted more by *resemblances* than by *differences*, and his systematic work is a presentation as essential and as valuable as some of the more detailed work which has followed him.

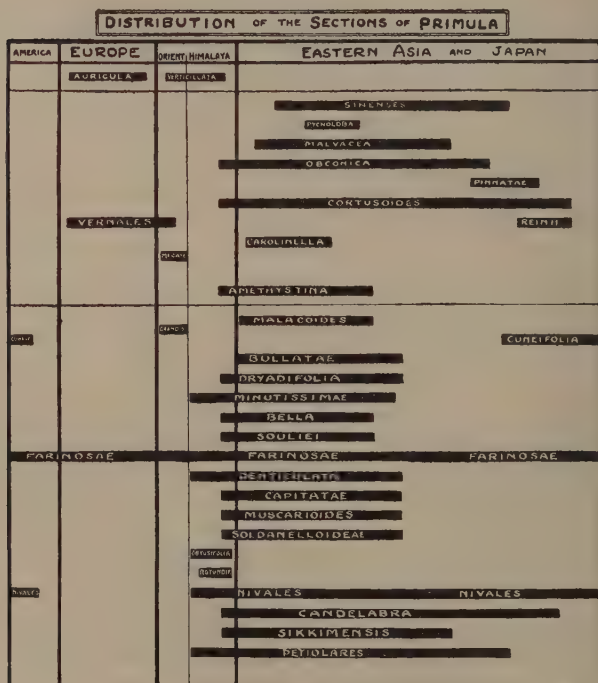
Traditional systematic practice as in the exemplar of Hooker did not then show any marked or any immediate response to the new ideas which came with Darwin and his contemporaries. The leaven worked slowly. Research based on experiment began to exercise an increasing effect. Analysis became much more detailed. *Differences* took precedence

over *resemblances*. But the main mass of systematic works between 1860 and 1900—and even later—did not show much change from the pre-Darwinian period. The systematist used for the most part the old criteria. Some of the tools were sharpened to a finer point, but they were the same tools. But there is now another invasion. Genetics and cytology have made great advances. The results of the new investigations penetrate deeply into a domain which the systematist was and is apt to think peculiarly his own. The opinions of his fellow-systematists are oftentimes hard enough to bear, but here is quite a new body of facts which have to be reckoned with. Once on a day when Humphrey Davy was making his discoveries of new elements, a Professor of Chemistry north of the Tweed, after his return from his usual annual sojourn of six months in delectable seclusion in the country—gone are these halcyon days,—took council of his assistant before resuming his classes with the query ‘Come along—tell me what has that awful man Humphrey Davy been doing while I’ve been away?’. And so in these days while engaged on a favourite genus one has to keep an eye on what the cytologists are doing.

It occurred to me therefore that it might be of interest to you to relate what an ordinary pedestrian systematist thinks of this new development and to tell you what is his reaction. It is necessary to choose common ground for the discussion of what may be divergent views. Consequently I am not going to lead you into the intricacies of *Rosa*, *Berberis*, *Salix*, *Triticum*, or *Oenothera*, for the very good reason that I would be a very incompetent guide therein. The challenged may quite well have the option of ground, and I have a predilection for *Rhododendron* and *Primula*. For reasons which I shall refer to later *Rhododendron* is not the choice—it would not be fair to the cytologist. But *Primula* has proved to be an exceptionally favourable genus for the comparison of views. In the first place without any knowledge whatever of the cytological data of the genus the late Mr. George Forrest and I drew up a few years ago a revision of the sections of *Primula* with citation of all the known species and their reference to what we considered their proper section. It is a large genus and it was divided into 32 sections. The divisions were made on purely morphological criteria—plus a knowledge of many of them in the field and in cultivation. For the cytological work I was very fortunate in interesting Dr. H. G. Bruun of Upsala in the numerous species of *Primula* in cultivation in Edinburgh, and on his visits there he secured material for his work. In his own words, his object was ‘to analyse the cytological conditions of a plant genus and the relations between cytology and taxonomy in this genus

and to determine if any cytological characteristics have a taxonomic value, and, if so, how far such characters prove useful and reliable for this purpose'. And, again, 'It would be especially useful if we could throw light on taxonomic problems by points of view derived from a department of research quite different from that taxonomists usually employ'.

DIAGRAM 1.

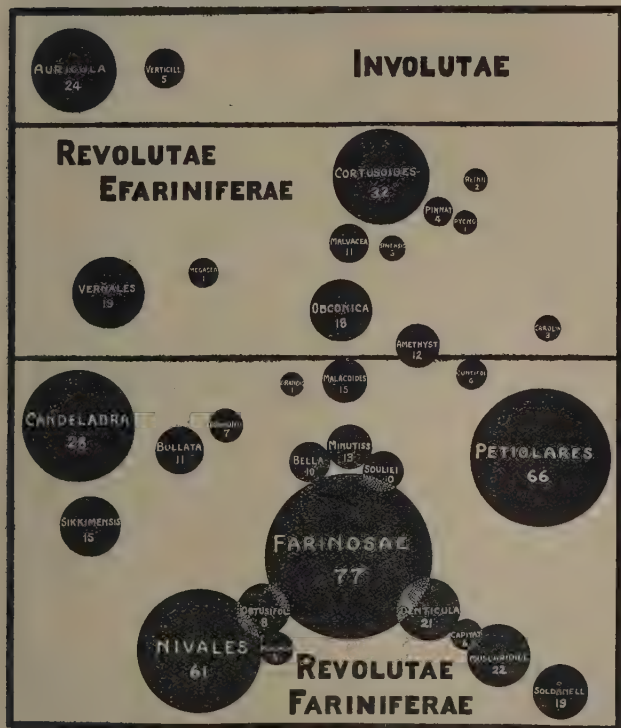


It is true that such comparisons have already been made in other genera. But the results have been very varied and often conflicting—at any rate, divergent,—and it is evident that we are still far from a clear understanding of the exact value of the new data. But, if only for the reason that the cytologist and the systematist have in this instance endeavoured to keep in touch, the comparison of their views may prove of interest. I must in the first place make it quite clear that Bruun has

endeavoured to base his conclusions primarily on the cytological evidence, although he is quite conversant with the taxonomic analysis. And I must make it equally clear that he does not claim that his analysis necessarily represents the

DIAGRAM 2.

THE SECTIONS OF PRIMULA



true phyletic position of the various species—only that on cytological grounds alone he would thus place them. We ought therefore to find a basis for comparison of the criteria on both sides of the question.

Advantages in the choice of *Primula* are that it is a large genus, that many of the species are in cultivation, and these have in most instances been grown from seeds collected

recently in their natural habitats, and that the genus in great part lends itself to division into quite distinct but more or less allied sections. Cytologically it exceeded expectations—in Dr. Bruun's opinion the best he has so far met with.

As regards geographical distribution, the genus finds its centre in Asia. Its predominance in Eastern Asia is well shown in diagram No. 1 (p. 154). The 32 sections are shown in diagram No. 2 (p. 155) where the relative size of each section is indicated; the numbers included show the total of species and subspecies in each. This arrangement is based entirely on morphological data. Modifications due to the influence of cytological data will be shown later.

Without going into details I merely mention that the chief morphological criteria used were: the folding of the leaves, the presence or absence of farina, the form of the corolla, petiolar development, lobing of leaf, sessile or stalked flowers, shape of capsule, rhizomatous development, presence of simple or of jointed hairs, etc. A reasonable amount of latitude was necessary in the employment of these criteria for the discrimination of the sections of the genus. Only one of them—the folding of the leaves—could be used absolutely. Variations from the normal had to be allowed for in the other differential sectional characters. As is the case in the analysis of other genera, the systematist cannot claim that his criteria can be applied rigidly. On his side Bruun found that his sections could be divided according to their nuclear constitution into different cytological types to which is given the name of karyotypes. For this analysis the genus proved very favourable. The criteria employed were (1) the number of the chromosomes, (2) size, (3) shape, (4) relative non-conformity of the chromosomes, and (5) location and appearance of constrictions and satellites. In the opinion of Bruun the sum of these cytological criteria was sufficient in any species examined to place that species in its proper *section* as judged solely by cytological analysis.

The results in so far as *Primula* is concerned appear to justify this conclusion. It is clear evidence of the quality and importance of this new method of analysis. Two problems suggest themselves. Firstly, can these cytological criteria be employed more rigidly than the ordinary morphological criteria, or must they be given a latitude in interpretation such as is found to be necessary in the latter? Secondly, if the analysis is carried beyond sectional values, to what extent will the cytological criteria be valid in the discrimination of species and in the assessment of degrees of affinity between species of the same section? Granted that there is a remarkable coincidence between the results of the two methods in so far as the broader issues are concerned, will there be the same

harmony when the investigations are carried into the field of greater detail?

Before proceeding to a comparison of the results of the two methods, I would like to refer to certain general points which may serve to elucidate what follows. While certain sections of the genus are more or less isolated and so morphologically easily defined, the boundary between others is much less definite. In diagram No. 2 such sections have been made to intersect. There was therefore the possibility that the cytological evidence would serve to solve at any rate some of these questions of affinity—that it would give information beyond the present reach of morphology. In the main—as has been the case in other genera—there is agreement between the taxonomy and the cytology of this genus. But interest lies in those cases where there is divergence of view. The taxonomically isolated sections are just those which show monomorphic karyotypes, while the difficult taxonomic sections tend to have variable karyotypes. Generally then, difficulties occurring in a taxonomic survey correspond to the same difficulties in a cytological survey.

But I hope to show cases where the cytologist is able to dot the i's and stroke the t's for the morphological analyst, and to give him certainty where formerly it was surmise. On the other hand, there are instances to be illustrated where the morphologist will hesitate—and with, I think, good reason—to follow his cytological guide.

I should also add here that it was soon evident that all species in the genus with the same chromosome number are not necessarily closely related. The same basic number occurs in several sections which are isolated from one another both in their morphological and in their cytological criteria. The diagram No. 3 (p. 174) illustrates that no reliance can be put on number only.

I can now proceed to my comparisons. Let us begin with the Vernales—the common primroses. It is an isolated section, morphologically and also geographically, as it does not reach either the Himalaya or China, the centre of the genus. Its cytological data show a great regularity:—

(Ex Bruun, Cyt. Studies in *Primula*, p. 124.)

	<i>n.</i>	<i>2n.</i>
Section Vernales.		
<i>P. juliae</i>	22	CHITTENDEN 1928, BRUUN 1930 b, HARRISON 1931
<i>P. vulgaris</i>	22	CHITTENDEN 1928, BRUUN 1930 b
<i>P. balearica</i>	22	HARRISON 1930, 1931
<i>P. heterochroma</i>	22	BRUUN 1930 b, HARRISON 1931
<i>P. sibthorpii</i>	22	HARRISON 1930, 1931
<i>P. amoena</i>	22	" " "
<i>P. leucophylla</i>	22	BRUUN 1930 b, HARRISON 1931

	n.	2n.	
<i>P. Ruprechtii</i>		22	HARRISON 1930
<i>P. elatior</i>	9		MARCHAL 1920
		22	BRUUN 1930 b, HARRISON 1931
<i>P. carpatica</i>		22	HARRISON 1930
<i>P. intricata</i>		22	" " " 1931
<i>P. Pallasii</i>		22	" " "
<i>P. pseudoelatior</i>		22	BRUUN 1930 b
<i>P. veris</i>	9		MARCHAL 1920
	11	22	DAHLGREN 1916
		22	CHITTENDEN 1928, BRUUN 1930 b,
			HARRISON 1931
<i>P. Columnae</i>		22	HARRISON 1930, 1931
<i>P. macrocalyx</i>		22	BRUUN 1930 b, HARRISON 1931
<i>P. Ingwerseniana</i>		22	HARRISON 1930, 1931
<i>P. Lofthousii</i>		22	" " " "
<i>P. pannonica</i>		22	" " " "
<i>P. rhododendricola</i>		22	BRUUN, publ. here
<i>P. Pazii</i>		22	" " " "
<i>P. vulgaris</i> × <i>Juliae</i>	11	22	CHITTENDEN 1928
		22	BRUUN, publ. here
<i>P. elatior</i> × <i>Juliae</i>	11	22	CHITTENDEN 1928
		22	BRUUN, publ. here
<i>P. vulgaris</i> × <i>elatior</i>		22	" " " "
<i>P. veris</i> × <i>vulgaris</i>		22	CHITTENDEN 1928, BRUUN, publ. here
<i>P. Juliae</i> × <i>veris</i>		22	BRUUN, publ. here
<i>P. Polyanthus</i> Cloth of Gold × <i>Juliae</i>	11		CHITTENDEN 1928
Section <i>Megaseaeifolia</i> .			
<i>P. megaseaeifolia</i>		22	BRUUN 1930 b
	11		HARRISON 1931

There is no polyploidy—not even in garden forms. It is cytologically isolated—no kinship with any other group can be shown cytologically. Morphologically its decurrent leaves separate it readily from what must be its nearest (if still distant) allies—the section *Cortusoides* and its associate sections. Yet *P. Juliae* is reckoned with the *Vernales* in spite of its orbicular leaf. Now comes in a point of some cytological interest. There is a peculiar species, *P. megaseaeifolia*, from Asia Minor, whose exact placing has long been uncertain. At one time allocated by Pax to his section *Sinenses*, in his monograph he removed it to *Carolinella*—a section of rather remarkable Chinese *Primulas* never in cultivation (a genus to Hemsley): this somewhat unhappy choice did not commend itself to Balfour (1913), who placed it in a section by itself, inclining to regard it as perhaps as isolated as *P. grandis*. Forrest and I, while retaining it as best in a section to itself, believed that it tended towards *P. Juliae* and so towards the *Vernales*. To some extent we were guided by its behaviour in cultivation, but we would no doubt be hard put to it to give reasons for our opinion. Cytology scores in placing it definitely in close relationship

with Vernales and leaving practically no room for argument. *P. megaseaeifolia* has two pairs of satellited chromosomes as compared with a single pair in Vernales, but it is in accord otherwise in its karyotypic characters—and has no relations with any other section. The distinction is slight and taxonomically the species could go into Vernales without prejudice.

The cytological analysis of the section Cortusoides is shown below :—

(Ex Bruun, p. 125.)

	<i>n.</i>	<i>2n.</i>
Section Cortusoides.		
Subsection Geranioides.		
<i>P. heucherifolia</i>	22	BRUUN 1930 b
<i>P. geraniifolia</i>	22	" "
<i>P. latisecta</i>	22	" "
Subsection Septemlobae.		
<i>P. Maclarenii</i>	24	" "
<i>P. septemloba</i>	24	" "
<i>P. mollis</i>	24	" "
<i>P. seclusa</i>	24	" "
Subsection Paulianae.		
<i>P. Pauliana</i>	24	" "
Subsection Eu-cortusoides.		
<i>P. cortusoides</i>	24	" "
<i>P. saxatilis</i>	24	" "
<i>P. Sieboldii</i>	24	IINUMA 1926, ONO 1927, BRUUN 1930 b, NAKAJIMA 1931
	36	IINUMA 1926
usually 16—20	36	ONO 1927
<i>P. polyneura</i>	24	BRUUN 1930 b
<i>P. hymenophylla</i>	24	BRUUN, publ. here
<i>P. lichiangensis</i>	24	BRUUN 1930 b
<i>P. Veitchii</i>	24	" "
Subsection Jesoanae.		
<i>P. jesoana</i>	13	MIYAJI 1929

It has not been possible to analyse all the species of this section cytologically, but of the species available Dr. Bruun indicates division into five subsections.

The complete list of the species of the section is given below and they are arranged according to their respective affinities as judged by morphological data. Only two sections are recognised, but the division could be carried further by keeping *P. mollis* and *P. seclusa* in a small subsection and *P. Pauliana* similarly. The main distinction between the two chief subsections lies in the leaf-venation, more or less pinnate in Eu-cortusoides and palmate in Geranioides :—

Subsection Eu-cortusoides.

- P. cortusoides* Linn.
- P. saxatilis* Komarov
- P. Sieboldii* E. Morren
- P. lactiflora* S. Turk.

P. Kaufmanniana Regel

P. polyneura Franch.

Subspecies.

P. hymenophylla Balf. f. et Forrest

P. lichiangensis G. Forrest

P. sataniensis Balf. f. et Farrer

P. sikuensis Balf. f. et Farrer

P. Veitchii Duthie

P. cinerascens Franch.

Subspecies.

P. sinomollis Balf. f.

P. sylvicola Hutch.

P. violodora Dunn

P. mollis Nutt.

Subspecies.

P. seclusa Balf. f. et Forrest

Subsection Geranioides.

P. kisoana Miq.

P. jesoana Miq.

P. Paxiana Gilg.

P. Maclareni Balf. f.

P. heucherifolia Franch.

Subspecies.

P. humicola Balf. f. et Forrest

P. geraniifolia Hook. f.

P. septemloba Franch.

P. alsophila Balf. f. et Farrer

P. latisecta W. W. Sm.

P. Minkwitziae W. W. Sm.

P. palmata Hand.-Mzt.

P. vaginata Watt.

P. eucyclia W. W. Sm. et Forrest

P. Normaniana Ward

P. Pauliana W. W. Sm. et Forrest

In the first place there is agreement morphologically and cytologically that the section *as a whole* is consistent in spite of the variation in the basic number of the chromosomes. But as regards the subsections the two sets of data are not in accord. The subsections as based on the cytology do not agree with the morphological criteria. Let us eliminate first some minor points of difference:—

(1) There would be no objection by the morphologist to placing *P. Pauliana* in a subsection to itself—it has a remarkable racemose inflorescence—but it is quite reasonably accommodated in Geranioides. It is, however, evidence of the fineness of the analysis that this species can be distinguished cytologically.

(2) The subsection Eu-cortusoides contains only one point of divergence in the respective views. The cytologist would remove *P. mollis* and *P. seclusa*. To this the morphologist would make no serious demur, as morphologically there is a certain difference between them and the other members of the

subseries. But the cytologist would refer them to the subsection Geranioides. The morphological criteria do not support that view.

(3) *P. jesoana* is too little known, while its nearest allies such as *P. kisoana* have not been investigated. Whether these Japanese species warrant subsectional grouping remains to be seen. The divergence of *P. jesoana* in basic number is not necessarily conclusive.

The main points at issue may be thus briefly stated:—

(a) the cytologist would remove *P. Maclarenii* and *P. septemloba* from association with *P. geraniifolia*, *P. latisecta*, and *P. heucherifolia*; (b) the cytologist would regard *P. mollis* and *P. seclusa* as phyletically nearer to *P. septemloba* and *P. Maclarenii* than these last are to *P. geraniifolia* and its allies.

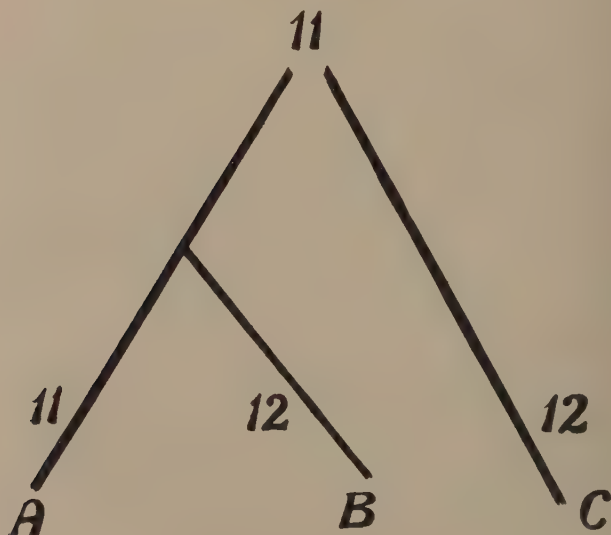
The criteria of the morphologist would lead him to the following conclusions:—

(a) *P. geraniifolia* and *P. septemloba* are exceedingly near morphologically—are, indeed, difficult to distinguish. He would not be inclined to give much weight to the difference in chromosome number in this case. There are other examples of allied species in *Primula* differing in this respect. *P. geraniifolia* occurs in the Eastern Himalaya, *P. septemloba* in Yunnan and Szechwan. There is no marked geographical separation.

(b) To the morphologist *P. mollis* and *P. seclusa* are much further away from *P. septemloba* and *P. Maclarenii* than these are from *P. geraniifolia* and *P. latisecta*. He would not regard *P. mollis* and its ally as being in the same subsection with *P. septemloba* and *P. Maclarenii*.

While therefore on broad general grounds the cytological data are in conformity with the morphological, the alignment of the species on the two sets of data would markedly differ. In the case under review the morphologist would undoubtedly demur to the conclusions of the cytologist. Whatever the numbers, trabants, etc., may indicate, they cannot be (to the morphologist, at any rate) the ultimate criteria. The cytologist here is inclined to be dogmatic also. The conclusion thus is, that *P. heucherifolia*, *P. geraniifolia*, and *P. latisecta*, provided with a different number of chromosomes are, in spite of the contradictory evidence of the morphological character, more closely akin to each other than to other species included in the section. This deduction is confirmed by the geographical distribution of these species, in that it appears to be orientated westward within the area of the section, being confined to the eastern slopes of the Himalaya Mountains, Eastern Tibet and Yunnan, while the rest of the subsection is distributed in Central and Northern China, Manchuria and Japan.' (Bruun, p. 26.)

I interpret the geography otherwise, but let that go. What is the evidence of the cytological characters? Surely, after all, the cytological characters have their expression in the morphological equipment—and this latter represents the meaning of these characters. The qualitative effect must be more important than the quantitative—the criteria of the latter must give place. As a solution in this case I am inclined to assume that two related species A and B may differ more from one another in their grosser karyological features than A and C, which are less akin. A and B may be the nearest allies phyletically and may have yet deviated—for various reasons—in their karyological characters:—



Too much must not be read into the grosser cytological phenomena. Approximation cytologically is not necessarily decisive as to close affinity. Until the cytologist can in this genus carry his analysis deeper, involving the *qualitative* content of the chromosomes and the different relationships between them, this divergence of opinion will persist. Experimental genetic studies may here aid, but *Primula* is not a genus likely to lend itself freely to inter-crossing except within comparatively restricted sections and subsections.

Allied to Cortusoides are several small sections—Reinii, Pycnoloba, Sinenses, Obconica. These sections are separated from Cortusoides and from one another by small morphological differences. The cytological data confirm, giving just and only just sufficient reason for keeping them apart. Pax was therefore very near the mark in including them, except Reinii, in the section Sinenses. Neither the morphological nor the cytological criteria are in any way decisive. But, again, we have evidence of the delicacy of the new instrument, for it may be of interest to note, as Bruun points out, that the cytological evidence disposes of the legend that the garden form of *P. obconica* has any admixture from *P. sinensis*. An outline of the cytological data is appended:—

(Ex Bruun, p. 125.)

	n.	2n.	
Section Reinii.			
<i>P. Reinii</i>	24		IINUMA 1926, BRUUN 1930 b
Section Pycnoloba.			
<i>P. pycnoloba</i>	24		BRUUN 1930 b
Section Obconica.			
<i>P. obconica</i>	11—12		MARCHAL 1920
	12	24	BRUUN 1930 b, PHILP (commun. 1929)
<i>P. obconica</i> f. <i>gigas</i>		48	PHILP (commun. 1929)
<i>P. obconica</i> × <i>sinensis</i> (pure <i>obconica</i> ?)	18		VOKOLEK 1925
<i>P. sinolisteri</i>		24	BRUUN 1930 b
<i>P. werringtonensis</i>		24	" "
Section Sinenses.			
<i>P. calciphila</i>		24	" "
<i>P. sinensis</i>	12	24	GREGORY 1909, KEEBLE 1912, SVERDRUP SÖMME 1930, DARLINGTON 1931
		24	VOKOLEK 1925, BRUUN 1930 b, DARK 1931
<i>P. sinensis</i> f. <i>gigas</i>	24	48	GREGORY 1914, SVERDRUP SÖMME 1930, DARLINGTON 1931
		24	BELLING 1927
		48	BRUUN 1930 b

My next illustrations will be taken from the Fariniferae. The morphological criterion of presence or absence of farina may at first sight appear to be one of doubtful validity, especially as within the Fariniferae must be included on other grounds species with no trace of farina and as even species are known which vary from farinose to efarinose. But the Efariniferae throughout show no farinose species, while efarinose species in Fariniferae tend to be exceptional. Cytology confirms segregation into these two groups and proves also that the inclusion of the special efarinose species

in Fariniferae is entirely justified. Support of this criterion is particularly welcome to the morphologist, for, as has been already indicated, few are the characters which can be used with any approach to absoluteness. It is, again, testimony to the close correlation between the two sets of data in sectional values.

It will be noticed in diagram No. 2 that certain small sections appear on or near the border-line—Amethystina, Cuneifolia, and Malacoides. This placing indicates the doubt in the mind of the morphologist as to their correct position. How far will the cytological data help to a decision? In the section Cuneifolia, formerly described as efarinose, there is a trace of farina. The morphologist, while regarding the section as somewhat isolated, favoured its inclusion within the Fariniferae. On the first analysis the cytologist considered that the karyotype differed sharply from previously described types and excluded the section quite definitely from any kinship with the Efariniferae. If any alliance could be indicated cytologically, the most plausible was with the section Auriculatae:—

(Ex Bruun, p. 128.)

	2n.		
Section Cuneifolia.			
<i>P. nipponica</i>	22	INUMA	1926
<i>P. suffrutescens</i>	44	BRUUN	1930 b
Section Inayatii.			
<i>P. Inayatii</i>	16	"	"
Section Auriculata.			
A. <i>P. algida</i>	44	"	"
<i>P. luteola</i>	44	"	"
B. <i>P. rosea</i>	22	"	"
<i>P. elliptica</i>	22	"	"

But since the reading of this lecture further data have come to light showing that morphologist and cytologist were equally in error. In all previous work on the genus it has been only too readily assumed that the only sections with involute leaves are Auricula and Verticillata. Herbarium specimens are rarely of service for detection of this character, and living material is not always available. I am therefore the more indebted to Mr. R. E. Cooper, Assistant Curator of the Royal Botanic Garden, Edinburgh, for his observations on the involution of the leaves of young growing plants of several of the Japanese species of this section and also for a similar discovery in a group of American Primulas, previously misunderstood and now clearly seen to be allied to the same section. I have already referred to the importance of this criterion as the one which may be regarded as absolute. Previous

placings of the section, whether based on morphological or on cytological data, are at once negated by this one primary observation.

It is clear that the section finds its true position among the *Involutae* and in alliance with *Auricula*. The morphological and cytological data are now seen to be in consonance with this arrangement. Dr. Bruun now agrees that *Cuneifolia* goes very well with *Auricula* cytologically. An interesting corollary is that the European section *Auricula* is no longer markedly isolated from other sections, as its nearest ally is the Japanese *Cuneifolia*, and this latter section is in its turn closely associated with American species to be grouped in a new section *Parryi*.

I should add that I have failed to find any references in literature to the involution of the leaves in *Cuneifolia*, but in the Report of the Primula Conference (R. H. S. Journal, xxxix, 1913, p. 178) Sir Isaac Bayley Balfour has remarked:— 'The section *Cuneifolia* presents us in Japan with specific forms which have a strong physiognomic resemblance to species of the European alps, but always without glands.' At that time these Japanese plants were not in cultivation and its phyletic association with *Auricula* was unsuspected.

From the cytological aspect the *Involutae* in Dr. Bruun's opinion would be arranged thus:—

Chromosomes very small.

Number 9—non-uniform	<i>Auricula</i> .
„ 11—rather uniform	<i>Cuneifolia</i> .

Chromosomes of medium size or smaller.

Number 9—slightly non-uniform	<i>Verticillata</i> .
„ 11—distinctly non-uniform	<i>Parryi</i> .

The section *Malacoides* has a basic number 9 and farina is usually manifest. While regarding this section as isolated and within the *Fariniferae*, I have been of the opinion that there is a suggestion of affinity with *Obconica*. But this resemblance is superficial, for to Bruun its cytology debars it from any alliance with *Obconica* and gives confirmation of the taxonomic importance of the character—presence or absence of farina. Yet its close affinity to any of the other farinose sections is in Bruun's view unlikely—cytologically. In this from the morphological side I would concur. Several of the sections among the *Fariniferae* are very definitely isolated.

The section *Amethystina* shows, as a rule, no farina, but there is a trace of it in some of the species. Its cytological characters have not been examined, but there is the likelihood that material of two species will soon be available. In all probability the section will come cytologically as well as morphologically within the *Fariniferae*. [This has been confirmed by the

analysis of *P. Kingii* and *P. amethystina* var. *brevifolia*. The karyotype is considered by Bruun to be very like or indistinguishable from that of *Petiolaes* and *Nivales*. Morphologically the association with these sections is not at all convincing.]

Of some interest is the solitary species *P. grandis*. It does not look like a *Primula*. Its cytology shows the smallest chromosomes in the genus and no similarity to any of the other karyotypes. Taxonomy and cytology are again in agreement, and on the evidence of both sets of data no present member of the genus would have a better claim to separate generic rank.

Of great importance is the consideration of the section *Farinosae*—the largest of all. Morphologically it is a puzzling section and admittedly not homogeneous. In his earlier work Pax divided the species into *Farinosae* and *Auriculatae* on the shape of the capsule; in his Monograph (1905, p. 70) and in agreement with Kusnetzow he joined them together again. They were separated again by Sir Isaac Bayley Balfour (1913), and perhaps in despair (1928) once more associated by Smith and Forrest. Although these numerous species were thus included in one section, it was recognised that they fell into several groups—some easily recognised and some not. But really good morphological criteria are lacking, if we are to judge by the want of agreement among the various commentators. The species as far as available in the living state have been subjected to the analysis of cytology. Frankly, the results are exceedingly illuminative. No longer is in this case cytology merely corroborative, but it goes beyond morphological analysis and is in a position to supply the much-needed criteria. Moreover, the results of the cytological analysis are such as command the acquiescence of the systematist—at least, I am convinced. Here are the cytological data:—

(Ex Bruun, p. 128.)

Section <i>Souliei</i> .	<i>n.</i>	2 <i>n.</i>	
<i>P. rupicola</i>	16		BRUUN, 1930 b
Section <i>Farinosae</i> .			
Subsection <i>Stenocalyces</i> .			
<i>P. stenocalyx</i>	16	" "	
<i>P. blandula</i>	16	" "	
<i>P. sertulum</i>	16		BRUUN, publ. here
<i>P. Knuthiana</i>	16		BRUUN 1930 b
<i>P. caldaria</i>	16	" "	
Subsection <i>Eu-farinosae</i> .			
<i>P. modesta</i>	18		NAKAJIMA 1931, BRUUN, publ. here
<i>P. Fauriei</i>	9		IINUMA 1926
	18		BRUUN 1930 b

	n.	2n.	
<i>P. farinosa</i>	9		MARCHAL 1920
	9	18	BRUUN 1930 b, 1932 b
<i>P. farinosa</i> f. <i>Warei</i>		72	BRUUN 1930 b
<i>P. exigua</i>		18	" "
<i>P. magellanica</i>		72	BRUUN 1930 b, 1931 a
<i>P. scotica</i>		54	" " "
<i>P. scotica</i> var. <i>scandinavica</i>		72	" " "
<i>P. stricta</i>	126		BRUUN 1930 b
<i>P. longiflora</i>		36	BRUUN 1930 b, 1932 b
<i>P. frondosa</i>		18	BRUUN 1930 b
<i>P. farinifolia</i>		18	BRUUN 1930 b
<i>P. capitellata</i>		72	" "
Subsection <i>Sibiricae</i> .			
<i>P. sibirica</i>		22	" "
<i>P. involucrata</i>		44	" "
<i>P. chrysopa</i>		20	" "
<i>P. yargongensis</i>		20	" "
<i>P. tibetica</i>		20	" "
<i>P. fasciculata</i>		18	" "
Subsection <i>Glabrae</i> .			
<i>P. Genestieriana</i>		16	" "
<i>P. glabra</i>		16	" "
Section <i>Yunnanensis</i> .			
<i>P. yunnanensis</i>		22	" "
Section <i>Minutissimae</i> .			
<i>P. reptans</i>		22	" "

The noteworthy points are as follows :—

(1) The cytological evidence is very clear on the major question of the separation of *Auriculatae* as a section distinct from *Farinosae*. This may be considered a final judgment. I might add that as far as the species are in cultivation, the experience of garden practice would approve the separation.

(2) In *Farinosae* (now relieved of the *Auriculatae*) the subsection *Eu-farinosa* stands out as a unit cytologically consistent. It has still the widest distribution; it has numerous instances of polyploidy; it has extended into the colder areas of Europe and America, and there usually in polyploid species or subspecies. Within *P. scotica* we find cytological differences comparable to what is seen in *Festuca ovina*.

(3) The separation of the subsection *Stenocalyces* is of particular interest. The *Farinosae*, in spite of their wide distribution, do not penetrate deeply into China, the centre of the genus. As for Dr. Bruun's *Eu-farinosa*, he shows that they do not occur within the confines of China. But morphologists have recognised that species such as *P. caldaria*, *P. sertulum*, and *P. Knuthiana* have a *facies* indistinguishable

from Farinosae and would certainly include them. Cytology shows that they may be taken into Farinosae *sensu lato*, but also that these Chinese species form a distinct cytological and geographical group. But to this doubtless valid conclusion the morphological data can contribute no definite evidence.

(4) In subsection Sibiricae we have a glabrous *efarinose* assemblage of species, *P. chrysopa* excepted; it is farinose and on morphological grounds would be put by me into a separate subsection Gemmifera. But although *P. chrysopa* (and its farinose allies not yet cytologically examined) would be thus separated morphologically, its inclusion by Bruun within the Sibiricae for cytological reasons is of considerable interest. The *efarinose* Sibiricae, at least in the Himalaya and in China, affect very moist habitats. This may be a reason for the evolutionary disappearance of the farina. In view of their cytology, they may quite well be derived from farinose ancestors of the character of *P. chrysopa*, while morphologically the distinctions between the two subsections are not of serious moment.

The divergence in basic number in the Sibiricae is remarkable yet cytology agrees with taxonomy in regarding the species as close allies in spite of these variations. Mere number may be very unreliable unless supported by other cytological data. In this connection the case of *P. yargongensis* (better known in cultivation as *P. Wardii*) is worth a comment. This plant differs from *P. involucrata* in colour of flower only—as far as morphology can guide. Yet they have distinct basic numbers. The taxonomist, however, would not agree to the disjunction of these two plants, as the morphology is unmistakable. Just as in the case of *P. geraniifolia* and *P. septemloba*, they have diverged cytologically, but phylogenetically they are very intimately connected.

(5) Diagnostic cytological data confirm the taxonomic position of section Souliei, of subsection Glabrae where the true position of *P. glabra* has always been open to doubt, and of subsection Yunnanensis which Dr. Bruun now agrees is better included in Farinosae *sensu lato*.

(6) Section Minutissimae is simply an assemblage of very minute species whose affinities are not clearly known, though cytology and morphology would probably agree in connecting them with Farinosae. But as only one species has been in cultivation, no general statement can be made.

We come now to calmer waters. With regard to the closely allied sections Denticulata, Capitatae, Muscarioides, and Soldanelloideae, Bruun remarks that these constitute the best example of coincidence between taxonomy and cytology. Morphologically it is easy to distinguish between these four

sections, although there is a general resemblance in the compacted inflorescences. Here is the cytological analysis:—

(Ex Bruun, p. 127.)

	n.	2n.	
Section Capitatae.			
<i>P. capitata</i>	18	BRUUN 1930 b	
<i>P. crispata</i>	18	" "	
<i>P. lacteocapitata</i>	18	" "	
<i>P. Mooreana</i>	18	" "	
<i>P. sphaerocephala</i>	9 18	" "	
Section Denticulata.			
<i>P. denticulata</i>	11 22	BRUUN 1930 b, 1931 b	
<i>P. erythrocarpa</i>	22	" "	
* <i>P. crispa</i>	44	" "	"
<i>P. "cachemiriana"</i>	52	BRUUN, publ. here	"
Section Muscarioides.			
<i>P. cernua</i>	20	BRUUN 1930 b, 1931 b	
<i>P. Menziesiana</i>	40	BRUUN 1930 b	
<i>P. bellidifolia</i>	20	" "	
<i>P. atricapilla</i>	20	BRUUN 1930 b, 1931 b	
<i>P. lepta</i>	40	BRUUN 1930 b	
<i>P. pinnatifida</i>	20	" "	
<i>P. apoclita</i>	40	" "	
<i>P. muscarioides</i>	40	" "	
<i>P. deflexa ?</i>	40	" "	
<i>P. cyanantha</i>	40	" "	
<i>P. Littoniana</i>	10 20	BRUUN 1930 b, 1931 b	
Section Soldanelloideae.			
<i>P. nutans</i>	20	BRUUN 1930 b	
<i>P. Wollastonii</i>	20	BRUUN, publ. here	
<i>P. Reidii</i>	20	BRUUN 1930 b	
<i>P. Buryana</i>	20	BRUUN, publ. here	

The chromosomes are identical in size and shape, but with different numbers, with the exception that there is no cytological distinction between Muscarioides and Soldanelloideae. Briefly the points of interest are:—

(1) The cytology shows that in my original diagram the indication of close affinity with Farinosae is too pronounced. They do not overlap.

(2) While Soldanelloideae is not cytologically distinguishable from Muscarioides, it is so morphologically, and to some extent culturally. In Soldanelloideae the corolla is bell-shaped and the lobes are not reflexed. But the close cytological relationship between the two sections suggests that the Soldanelloideae have evolved from Muscarioides-like ancestors. The drooping bell-like corolla is of frequent occurrence in various genera in the wetter areas of the East Himalaya and of West China.

(3) Dr. Bruun remarks that apparently in Muscarioides polyploidy is devoid of taxonomic value.

* Amended 18 (Bruun 1932 in litt.).

(4) *P. capitata* was described in the 'Botanical Magazine' in 1850 by the elder Hooker. In the 'Flora of British India' the son retains it as separate from *P. denticulata* with hesitation. Now that both are well known in cultivation, the species are recognised as very different from one another. Their times of flowering and their cultural behaviour are also quite unlike. This taxonomic opinion is confirmed by the cytology. The case of *P. crispa* is peculiar. (More correctly it should be called *P. glomerata* Pax—a prior name.) It has always been associated with *P. denticulata* and its immediate allies. Culturally it behaves as the Capitatae. The first cytological analysis was based on material incorrectly referred to *P. crispa* and favoured the traditional view. But a further examination of the true species gives a count of 18 and brings it into harmony with Capitatae.

The remaining sections show great regularity. Here is the analysis of the Nivales:—

(Ex Bruun, p. 126.)

Section Nivales.	2n.	
A. <i>P. leucops</i>	44	BRUUN 1930 b
<i>P. Ellisiae</i>	44	" "
<i>P. Parryi</i>	44	" "
<i>P. Rusbyi</i>	44	" "
B. <i>P. Maximowiczii</i>	22	" "
<i>P. tangutica</i>	22	" "
<i>P. szechuanica</i>	22	" "
<i>P. obliqua</i>	22	" "
C. <i>P. macrophylla</i>	22	" "
D. <i>P. russeola</i>	22	" "
<i>P. sinoplantaginea</i>	22	" "
<i>P. melanops</i>	22	" "
<i>P. chionantha</i>	22	BRUUN 1930 b, 1931 b
<i>P. Purdomii</i>	22	" "
Section Rotundifolia.		
<i>P. Gambeliana</i>	22	" "

The uniformity in general is indisputable. Attention may be called to the following points:—

(1) The cytological data have been used to suggest sub-sections. These in the main are in accord with the morphology.

(2) The American species, *P. Ellisiae*, *P. Parryi*, and *P. Rusbyi*, have a facies of their own morphologically, but present cytologically a marked resemblance to *P. leucops*, a Chinese species. But *P. leucops* has no obvious morphological connection with these American species. Its links are clearly with *P. sinoplantaginea* and other Chinese species. In spite of the cytological approximation, it is not phyletically near *P. Ellisiae* and its allies. The two sets of data for the section are in accord for sectional values, but not for the alignment

of species within the section. On this group of four species Bruun remarks:—‘Of course they should be divided into two subsections, if other characters so demand, but, as has been stated, cytology does not show any reason for this’. (Bruun, Cyt. Stud. p. 90.)

Cytologist and morphologist are here at variance as to the placing of the three American species quoted. Both agree in regarding them as coming within the section. It has now to be recorded that both are quite wrong—in spite of the apparent congruity of the morphological and cytological data. Living plants of the three species are available and, as in the case of *Cuneifolia*, the folding of the leaves is involute. The observations of Mr. Cooper on this point are quite conclusive. These species have no phyletic connection with the *Nivales*. They form a section—*Parryi*—closely linked to *Cuneifolia* and separated from it only by minor morphological and cytological characters. Even as in *Cuneifolia*, a primary sectional criterion, previously unobserved, disposes of the argument, and shows conclusively that it is very easy to go astray in the application of cytological as well as of morphological data. Moreover, these same data are now seen to be in accord with the new alignment. In addition to the above three American species, the new section *Parryi* will include *P. angustifolia* Torr. and *P. Cusickiana* A. Gray. Involution of the leaf has been observed in living plants of the former and in dried material of the second.

(3) It is of interest that the Himalayan species *P. macrophylla*, with difficulty distinguishable morphologically from Chinese allies like *P. sinoplantaginea*, shows some degree of cytological difference—beyond these allies *inter se*.

(4) The section *Rotundifolia* is in its cytology clearly of *Nivalid* affinity. Its association with the section *Nivales* has been indicated in recent taxonomic work on the genus. But the character of the orbicular leaf with distinct petiole has been used in rather absolute a fashion (e.g. Pax, Monog. p. 120) and the result has been the juxta-position of species which have no real affinity. The cytological evidence in its bearing on sectional values is here of very special service. Cytology confirms the view that the well-marked criterion of the orbicular leaf is no barrier to alliance with the very different leaf of the typical *Nivales*.

(5) A peculiar species, *P. Inayatii*, was included by Smith and Forrest among the *Nivales*. On the cytological evidence it is shown by Dr. Bruun to have no affinity whatever with that section and is given a section to itself. As an alternative the taxonomist would be inclined to favour placing it somewhere among the *Farinosae*, but the cytological data are in opposition also to that view. The cytologist is probably

right in keeping the species outwith either of the two sections.

(6) The homogeneity of the Nivales in their cytology is likely to be lessened on analysis of species not yet examined—for a recent count in *P. pulchella* gives 16 and not 22.

The section Sikkimensis is uniform, as is well shown in the analysis:—

(Ex Bruun, p. 127.)

Section Sikkimensis.		n.	2n.
A.	<i>P. vittata</i>	22	BRUUN 1930 b
	<i>P. secundiflora</i>	22	" "
B.	<i>P. Waltonii</i>	22	" "
	<i>P. prionotes</i>	22	" "
	<i>P. Florindae</i>	22	" "
	<i>P. microdonta</i> var. <i>alpicola</i>	22	" "
	<i>P. microdonta</i> var. <i>violacea</i>	22	" "
	<i>P. reticulata</i>	22	BRUUN, publ. here
	<i>P. firmipes</i>	22	BRUUN 1930 b
	<i>P. flexilipes</i>	22	" "
	<i>P. sikkimensis</i>	22	" "
	<i>P. pseudosikkimensis</i>	11	22 " "
	<i>P. pudibunda</i>	22	" "
	<i>P. didyma</i>	22	BRUUN, publ. here

It is tribute to cytological discrimination that *P. vittata* and *P. secundiflora* are regarded as a little away from the others. This is in accord with the taxonomic characters.

The section Candelabra is likewise uniform. It is cytologically near the Nivales, but morphologically, geographically and culturally it is not. I regard the section as isolated. It will be noted that the cytologist places *P. ianthina* apart from its allies. This species is found on the extreme west of the area occupied by this section. Although it is not morphologically aberrant, its geographical separation is apparently linked with a degree of cytological difference:—

(Ex Bruun, p. 126.)

Section Candelabra.		n.	2n.
A.	<i>P. ianthina</i>	22	BRUUN 1930 b
B.	<i>P. Morsheadiana</i>	22	" "
	<i>P. melanodonta</i> ?	22	" "
	<i>P. serratifolia</i>	22	" "
	<i>P. Beesiana</i>	11	22 " "
		22	RICHARDSON 1930
	<i>P. burmanica</i>	11	22 BRUUN 1930 b
	<i>P. aurantiaca</i>	22	BRUUN 1930 b
	<i>P. Bulleyana</i>	12	MARCHAL 1920
		11	22 BRUUN 1930 b
		22	RICHARDSON 1930
	<i>P. Cockburniana</i>	22	BRUUN 1930 b, RICHARDSON 1930
	<i>P. chungensis</i>	22	BRUUN 1930 b
	<i>P. pulverulenta</i>	22	BRUUN 1930 b, RICHARDSON 1930
	<i>P. japonica</i>	22	INUMA 1926
		44	BRUUN 1930 b, RICHARDSON 1930

	n.	2n.	
<i>P. Miyabeana</i>		22	BRUUN 1930 b
<i>P. imperialis</i>		22	" "
<i>P. helodoxa</i>		22	" "
<i>P. Smithiana</i>	11	22	" "
<i>P. anisodora</i>		22	" "
<i>P. Poissonii</i>		22	" "
<i>P. Wilsonii</i>		22	" "
<i>P. pulverulenta</i> × <i>Cockburniana</i>		22	RICHARDSON 1930
<i>P. Bulleyana</i> × <i>Beesiana</i>		22	" "
<i>P. Bulleyana</i> × <i>pulverulenta</i>		22	BRUUN, publ. here

Sections Auricula and Verticillata have been studied by various cytologists. Taxonomically Auricula has in the past been regarded as an isolated section, but it is now clear that there is a decided affinity with Cuneifolia and Parryi. But that comment apart, Dr. Bruun and I have nothing to add to the record, not having studied Auricula in any detail. The prevalence of hybrids in Auricula is noteworthy. Hybridity is very rare or wanting in the other sections—at any rate, in the field. But in cultivation a section such as Candelabra is readily hybridised.

GENERAL CONCLUSIONS.

(1) It will be seen that in the first place there is a remarkable degree of agreement between the taxonomy and the cytology. This has been found to be so by investigators in other genera. While to a great extent the cytological data confirm the taxonomy, it is clear that they can be used very satisfactorily in criticism of the taxonomy and can supply in certain instances information beyond the reach of ordinary analysis. This agreement *in general* between the morphological and cytological analyses is not to be interpreted in the sense that the cytological evidence is superfluous; it is very clear testimony to the importance as well as to the accuracy of the cytological criteria—where the conditions are favourable to their application.

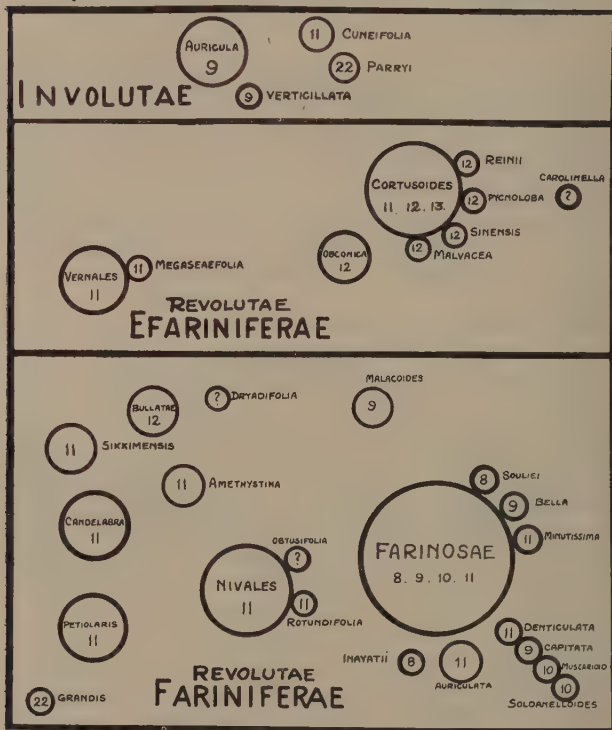
(2) The karyological characters in this genus are particularly favourable for detailed comparisons. Of these in Dr. Bruun's opinion the average size of the chromosomes was found to be the most constant. It is evident therefore that such genera as present definite features in their cytology, going beyond mere number of chromosomes, will prove a very valuable field for research, and the results there should go a long way to confirm or to modify the taxonomic analysis.

(3) The review shows how very misleading the mere record of chromosome numbers would be for phyletic purposes if additional karyological data had not been available. In

diagram No. 3 I have re-arranged to some extent my presentation of the sections. The relative size of the rings is roughly in accordance with the number of species in each section. The basic numbers of each section have been inserted (instead of the number of species as in diagram No. 2, p. 155). It is abundantly clear that any arrangement of the sections based on

DIAGRAM 3.

PRIMULA CHROMOSOME NUMBERS



number alone would be entirely at variance with the taxonomy and could not for one moment be defended. Consequently in genera where there is little or nothing to go on except chromosome number, much caution would need to be exercised in using number as a main principle in the grouping of species (or genera) into phyletic associations. On the evidence

afforded by *Primula*, the taxonomist may be pardoned if he cannot always regard this criterion as one of fundamental importance.

Since this was written my attention has been called to a paper by N. P. Ardulow on Karyo-systematic investigations on the Family Gramineae (Suppl. 43, Bull. Appl. Genet. & Plant Breeding, 1931) of which I have read a summary in English. The author points out how mere chromosome numbers are of secondary systematic value, whereas the methods of Levitsky, studying the chromosome morphology, etc., have produced very considerable elucidation both of the systematics and of the phylogeny and inter-relationships of many groups.

If, then, we cannot accept number as a final argument for the sections, is it to be regarded as an important criterion when we come to the allocation of species within a section? Not necessarily so. In the section *Cortusoides* and subsection *Sibirica* of *Farinosae* we have examples of closely allied species with different basic numbers. I quote (Bruun, p. 113) the cytologist:—‘In both cases the majority of the chromosome numbers are represented by several well-stabilised species and here, despite the opinion of taxonomists, we must probably bring each respective basic number under its own group, though these are probably phyletically closely allied.’

In dealing with these two instances I have stated that I differ. It is only fair to say that Dr. Bruun is himself alive to the inadequacy of mere number (Bruun, p. 116). Within certain sections the determination of the number is very illuminative—in other sections it has lost its validity. Dr. Bruun admits that a variation in the basic number of a morphologically similar group does not warrant the conclusion that the group is polyphyletic—for species obviously allied differ.

Consequently I have formed the impression that the broad cytological data are of much greater service for *sectional* values than for the alignment of closely related species. This is certainly the case in *Primula*. A group of distinct species may show no obvious cytological variation, while the same species may show forms differing in chromosome number (*P. scotica* and *P. involucrata*) or (what is the same thing) two very close allies may be cytologically different in chromosome number, but scarcely divergent morphologically. Therefore, while the morphologist can no longer ignore the cytology, it is incumbent on the cytologist to be able to appraise the morphology from the morphologist's point of view. Otherwise he too will have his own errors ‘of the cave’.

(4) It has already been noted that taxonomy and cytology

are here in agreement for the main issues. Where the section is isolated morphologically, it is also isolated cytologically. Sections which are difficult to define morphologically from their neighbours are also cytologically closely akin. The cytologist points out (Bruun, p. 117) that the sections do not prove to be equivalent from a cytological point of view. It has to be admitted that these sections are not equivalent from the morphological side. This criticism can be met by arranging the sections into larger groups corresponding to subgenera. Dr. Bruun has done this from the cytological point of view (p. 123 etc.), making 11 main groups of those sections which have been available for examination. With a few exceptions the morphologist would tend to agree to these *major* divisions of the genus as in accordance with the taxonomy.

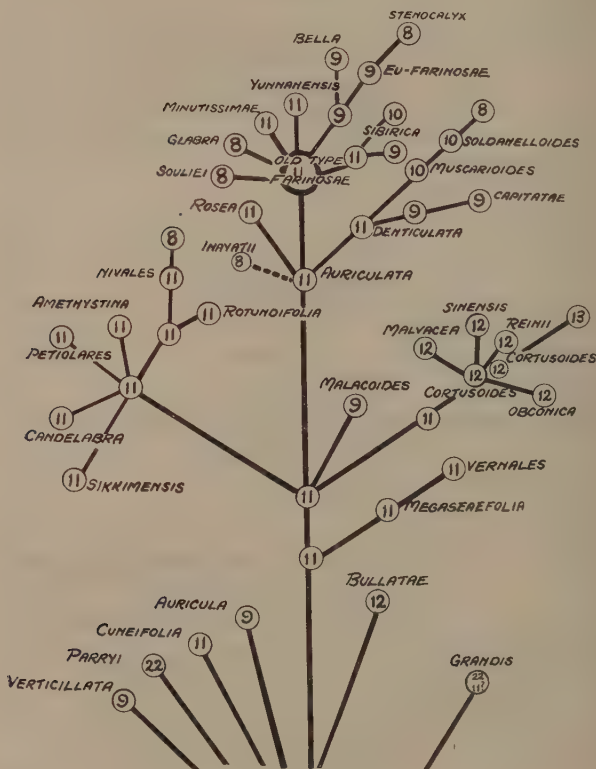
(5) It also appears that certain sections, to judge from chromosome number, seem to be more or less stabilised, while others are undergoing development and change. But I doubt whether there is any necessary correlation between these changes in number on the one hand and the frequency of new species on the other. It is easy to point to sections prolific in species such as *Farinosae* and *Cortusoides* where divergence in number of chromosomes accompanies specific difference. But in the sections *Nivales*, *Sikkimensis* and *Candelabra*, where the karyotypes are remarkably constant, that constancy has been no barrier to the free production of specific units. Multiplicity of species within a section—or within a genus—need not therefore be dependent on a variation in the number of the chromosomes nor on any very evident variation of the karyotype (i.e. as far as a general analysis can show, for modification of the factors must have taken place).

(6) In diagram No. 3 is given the arrangement of sections as modified by the cytological evidence. Comparison with diagram No. 2 will indicate the agreements and the changes which have been made. The cytological evidence has induced the taxonomist to make the following re-arrangements:—

- (1) Section *Megaseaefolia* is brought into close touch with section *Vernales*.
- (2) The sections which are allied to *Cortusoides* are placed much nearer that section.
- (3) Sections *Farinosae* and *Auriculata* are no longer combined. *Auriculata* is restored to sectional rank.
- (4) Section *Nivales* has been taken further away from section *Farinosae*. *P. Inayatii* is allotted to a section of its own.
- (5) Section *Denticulata* has been dissociated from actual contact with Section *Farinosae*.

It occurs in nearly half of the species investigated. This is the basis of a claim that the number 11 was the starting-point of *Primula* proper after the divergence of *Auricula* and *Verticillata*. The evidence certainly points that way. Dr. Bruun has kindly supplied me with diagram 5, which gives his view of the evolution of the genus. The successive alterations in

DIAGRAM 5.



Evolution of Sections.

basic number are therein indicated. This is a very interesting presentation, but Dr. Bruun wisely adds the *caveat* that the diagram is much more definite than our knowledge.

The general association of the sections in diagram 5 is in accord with the taxonomy, but the conclusion is drawn that the *Farinosae* must be a relatively young branch of the genus.

This may be so, but it is difficult to correlate this view with the wide and discontinuous distribution of this section as compared with all the other sections where continuity is the rule. It would be a very difficult task to appraise the relative age of the sections morphologically, and in this endeavour cytology may well be a more efficient weapon.

(8) Comparison with other genera seems to indicate that *Primula* is a genus remarkable for lack of uniformity in its cytological characters and so particularly suitable for analysis. Jørgensen (1928) arranges the genera which have been studied cytologically into three sections: (1) those with the same chromosome number in their species, (2) those with haploid numbers, and (3) those with numbers in multiple relations. It is evident that in *Primula* we have a combination of all three types. Genera apparently differ enormously in their degree of cytological variation. This is not surprising to the morphologist, for genera (as defined) have not equal values and cannot have. Generic criteria vary from family to family and can be established only by analysis. No generalisation is possible morphologically—nor cytologically. The cytological criteria will have different taxonomic values in different genera. It is also evident in many cases that a change in the morphology is not necessarily accompanied by any readily recognisable change in the cytology—and that a divergence in the cytology is not necessarily accompanied by a marked change in the morphology.

(9) Polyploidy does not appear to exercise any decisive effect in the genus, although it occurs in various sections. In this connection I would cite the interesting conclusions of Dr. Irene Manton in a recent paper (Ann. Bot. 1932) on the Cytology of the Cruciferae. In her opinion high polyploidy (p. 539), however much it may figure in elaboration of specific forms, is a barrier to true progress. In her view two distinct evolutionary processes appear in the Cruciferae—multiplication of forms and progressive evolution—associated respectively with polyploidy and aneuploidy.

(10) Obviously much will depend on the degree of differentiation in the cytological characters as to how far they are to influence the taxonomic view. In *Primula* the cytological data are remarkably exact. I mentioned earlier the genus *Rhododendron*. The contrast between them is noteworthy. Here we have two genera on approximately the same botanical horizon, occupying almost the same geographical areas, both very rich in species. In the one case the genus is divided into some 30 sections—cytologically distinct—and the species of different sections do not intercross. The genus *Rhododendron* can be broken up into about 40 sections—cytologically (as far as known) similar. Hybrids between species of different

sections are very common in cultivation. The cytological correspondence may well explain the facility in hybridisation. In a recent paper (Am. Journ. Bot. xvii. 1930, p. 247) Sax analyses a wide range of species of *Rhododendron* and finds a remarkable conformity in the number and character of the chromosomes.

‘The fact that there is complete or almost complete pairing of chromosomes in hybrids between Oriental and American species indicates that in *Rhododendron* at least the chromosomes are very stable in their genetic constitution over very long periods of time.’ (Sax, p. 250.)

Without the discovery of finer analytic methods it would appear that here cytology can aid the taxonomist to a very limited extent. Nevertheless, the morphological criteria for division into sections are as adequate as in *Primula* and afford more evidence of the relative age of the sections than is the case with *Primula*.

Clearly then in certain genera specific evolution has been accompanied by profound changes in the number and character of the chromosomes—in others not. Where chromosomic divergence is manifest, it is clearly of value as a criterion of difference—but it is not necessarily a criterion of degree of difference. Chromosomic divergence may run parallel to morphological divergence—or it may appear to be in excess within one genus—or it may be negligible within a genus or within allied genera. It is not a *measure*.

A striking example of non-divergence has just come to my notice in vol. xiv (1933) no. 1, Journ. Arn. Arbor., where McKelvey and Sax discuss the cytology of *Yucca* and *Agave*. Both have 5 pairs of large chromosomes and 25 pairs of small ones at meiotic division—and they are *similar* in both genera. And yet *Yucca* belongs to Liliaceae and *Agave* to Amaryllidaceae. Moreover, the variability within and between species of *Yucca* is not correlated with any variation in chromosome number or irregularity in chromosome behaviour.

Reference too should be made to a paper on *Anchusa* by S. G. Smith in Bot. Gaz. vol. xciv (1932), p. 394. In his studies on the Boraginaceae Dr. Johnston has seen reason from the morphological data to separate from *Anchusa* the genera *Brunnera* and *Caryolopha* (Johnston, Studies in the Boraginaceae.—III., Contrib. Gray Herb. Harv. Univ. lxxiii, pp. 42-78, 1924). Material of these two genera and of kindred species of *Anchusa* has been examined cytologically by S. G. Smith. According to the author the removal by Johnston of *Brunnera macrophylla* from the genus *Anchusa* is substantiated by the number and character of its somatic chromosomes. Similarly with *Caryolopha* (p. 402). I have no title to challenge these conclusions, but it must not be assumed that cytological

distinctions are necessarily an arbiter in estimating the status of genera. Obviously it would be easy to break up *Primula* into separate genera and to support the division by cytological data. These data have often a value as sectional criteria, but they are not to be taken as they stand as indications of generic diversity. Conversely, if two genera separable on morphological data are found to be identical in the grosser cytological details, that is no argument for combination into one genus.

(11) Let me conclude with a quotation (p. 219) from Dr. Bruun. 'In respect of the taxonomic-cytological relation of *Primula*, it may, on the whole, be said that the results of comparative karyology have been found of at least as great importance for taxonomy as reliable morphological characters.' For the reasons indicated I cannot go quite so far in this testimony to the accuracy of the cytological data. I believe that the last word lies with the morphology. But I can record without hesitation my obligations to the cytologist. His contribution has been of the greatest interest and value. But only by marshalling *all* the data, morphological and cytological, can a final judgment be made. In such a conclusion we are but in accord with previous workers (*cf.* Babcock in *Cyto-Genetics and the Species*, p. 11, Amer. Nat. lxxv, 1931). The main purpose of this lecture is to illustrate the co-operation which may be secured between two very different methods of attack on the taxonomy of a genus.

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OBITUARIES

SPENCER HENRY BICKHAM (1841-1933) was born near Manchester, and studied at Owens College and under Leopold H. Grindon (1818-1904), the botanist and writer on natural history. He was an early member of the Manchester Literary and Philosophical Society, and remained a member to the time of his death. As a young man he travelled extensively abroad on botanizing expeditions. He was elected F.L.S. in 1896, and was occasionally seen at the Society's Meetings.

Prior to taking up his residence at Underdown, Ledbury, in 1891, he was a member of a Manchester business firm and lived at Alderly Edge. He was thrice married, his three wives having predeceased him. His six daughters and one of two sons (all by his first wife) survive him.

From the account in 'The Ledbury Reporter and Guardian', 15 April, from which we quote, it is apparent that Bickham was not only the most prominent, hard working and highly esteemed resident 'within living memory', but, 'retaining his faculties in exceptional degree, he led a life of astonishing activity for one of his age. Keen, alert, regular and punctual in all his manifold activities, he lived for his work, which he was able to continue until a few months ago'. In the Rector's tribute at the Parish Church on the following Sunday we read that 'for 14 years S. H. Bickham held the Bishop's license as a lay reader, and delighted to read the lessons at Matins until he turned the wonderful age of four-score years and ten. . . . He served on innumerable public bodies, of which almost without exception he was chosen as Chairman'.

He died on 7 April 1933, aged 92, at 'Underdown', Ledbury. After a service at Ledbury Church on 11 April the funeral was at Bowden Parish Church.

He was a man of unusual versatility, for, apart from his love of botany and horticulture, he was also deeply interested in archæology and astronomy. He took a great and active interest in education, and as a Magistrate for forty years (being latterly Chairman of the Ledbury Bench) 'his decisions were always just and tempered with mercy'.

In his beautiful gardens at Underdown he grew a vast number of plants from various parts of the world; and it was his keen delight to take visitors to see these, and particularly his fine rock-garden.

Bickham refrained from frequently rushing into print. Apparently a short note on '*Silene noctiflora* in Worcestershire' was his first in the 'Journal of Botany' (1903). This was followed, up to 1917, by half-a-dozen more notes, the only paper of more than a page being that in 1913 on 'Carnarvonshire Plants'. This was in collaboration with E. S. Marshall

and W. A. Shoolbred, after their three weeks' visit to Capel Curig in July 1912. E. F. Linton was a member of the party for ten days. In 1916 came Bickham's 'William Peete and his Herbarium'—a page of interesting matter about the herbarium of William Peete (1771-1848) which he had bought. In 1917 appeared an interesting and important page on '*Carex pseudo-paradoxa* S. Gibson'.

He was an active and valued member of the two Botanical Exchange Clubs, and his numerous specimens were beautifully prepared. He was Treasurer to the Watson Exchange Club for thirteen years, and in 1906-7 officiated as Distributor. To that club alone he sent 5150 sheets of specimens, or an average of 224 in twenty-three years. All this was done between the age of 60 and 83, and notwithstanding his prodigious activities in other spheres. H. S. THOMPSON.

GILBERT CHARLES BOURNE, born in 1861, the son of Lt.-Col. Robert Bourne of the 54th Regiment, showed even at Eton the three interests which mainly filled his later life—rowing, soldiering and biology, the last being greatly stimulated by Philip Carpenter, then a master. Going up to New College, Oxford, in 1881, he was soon attracted by the personality of Prof. H. N. Moseley, the 'Naturalist on the *Challenger*', then Linacre Professor of Zoology, who seemed almost unconsciously to inspire in his pupils the feeling that research was the one thing worth doing in life. Before his final schools Bourne worked for a semester with August Weismann at Freiburg in Breisgau. After taking a first class in Zoology in 1885 he spent some months on a coral island, Diego Garcia, in the Chagos group, working at the Madreporaria and other forms on which Moseley was an authority, and studying atoll formation from a zoologist's standpoint; in a paper presented to the Royal Society he emphasized the action of marine currents in the production of atolls, and concluded that neither the views of Darwin nor of Murray were universally applicable to these islands. The experience of practical marine zoology thus gained was valuable to him when in 1887 he was appointed as the first Director of the Laboratory of the Marine Biological Association at Plymouth; the impetus which his energy and organizing power gave to the infant Laboratory has perhaps been insufficiently recognized. After a brief experience of City life, with which he felt little sympathy, Bourne returned to Oxford in 1892 as Assistant in the Zoological Department under Ray Lankester, became later Fellow and Tutor of New College, and finally Linacre Professor in 1906; retiring in 1921, he received the distinction of Emeritus. He was elected a Fellow of the Royal Society in 1895.

Of his fame as an oarsman, and particularly as a rowing coach, it is not necessary to write here. A keen soldier, he was at various times Lt.-Col. of the Oxford University Rifle Volunteers and of the 4th Battalion King's Shropshire Light Infantry, held a command at the Curragh Camp during the Boer War, and was engaged in training troops during the recent war. But these and other outdoor activities contributed to his scientific equipment, for his hard physical fitness ensured that coordination of hand and eye which made him a beautiful dissector and draughtsman.

Bourne's first paper, on the anatomy of *Sphaerotherium*, was communicated by Ray Lankester to this Society in 1885, and he was elected a Fellow in 1886; he served twice on our Council, and was Zoological Secretary from 1912 to 1915. Papers on *Fungia* and other Madreporaria, *Heliopora* and *Edwardsia* show that his early love for the Anthozoa always remained, and he contributed the Anthozoan section to Lankester's 'Treatise on Zoology' in 1900. Bourne also translated Pelseneer's general work on Mollusca, to form a volume of the same 'Treatise'; this drew his attention to a fresh group, in which he did a good deal of research, notably on Neritacea. Among his Crustacean papers an exhaustive study of the relations of the Raninidæ to other Decapodous Crustacea was communicated to this Society. Besides the very numerous papers in scientific journals Bourne published a useful 'Introduction to the Study of the Comparative Anatomy of Animals' in 1900, and a 'Text Book of Oarsmanship' in 1925. Always ready to undertake public service, he was at different times on Committees or Boards of the War Office, the Ministry of Agriculture and Fisheries, the Development Commission, and the Department of Scientific and Industrial Research, of the three last as a sequel of the interest in Fisheries which he acquired in early days at Plymouth and never lost.

The most characteristic facet which Bourne presented to the world was a steady resoluteness; he saw exactly what he wanted for his department, his college, or whatever it might be, and never spared himself in its pursuit. If he sometimes found it hard to suffer fools gladly, yet he was always popular among very diverse kinds of men, and a most steadfast friend.

G. H. FOWLER.

HERBERT CLIFTON CHADWICK, who died on 16 September 1932 at the age of 73, will be remembered by hundreds who have worked at the Port Erin Biological Station during the last thirty-four years.

He was born in Manchester on 21 September 1856. In his eleventh year he was sent to a boarding-school at Sale,

Cheshire, and there received at the hands of the master, a man of exceedingly ungovernable temper, injuries which incapacitated him for several years. When his health was in great part restored his great ambition was the profession of medicine; but circumstances led him into business, very much against his own inclination. He kept to business for upwards of twenty years, but during the whole of this time every available moment was devoted to the study of animal physiology and zoology, and he attended the evening classes conducted by the late Professors Gamgee, W. C. Williamson, and A. Milnes Marshall in the Owens College, Manchester.

Starting his career as a business man in Manchester, Chadwick was one of the group of amateur naturalists who were attracted by the formation of the Liverpool Marine Biology Committee, and who, under Herdman's leadership, did so much pioneer work on the fauna and flora of Liverpool Bay. Chadwick began his work on Echinoderms at the Committee's first Biological Station on Puffin Island, and from the time that the Port Erin station opened in 1893 he spent each summer holiday working there. In 1895 he was appointed a Curator at the Museum at Bootle. In 1898 he went to Port Erin as Curator of the Station, a post which he held until forced by failing health to give up most of his active work.

While interested in all marine life his own investigations were almost exclusively on Echinoderms, and most of his publications are on the morphology of this group. His four memoirs for the Liverpool Marine Biology Committee on *Echinus*, *Antedon*, *Asterias* and Echinoderm larvæ will remain as a lasting memorial to those who have known and worked with him, while a number of shorter papers and notes on the Echinoderms of the L. M. B. C. district have appeared from time to time in the Committee's reports and elsewhere. He also collaborated with Johnstone and Scott in a book 'The Marine Plankton', which was published in 1924. In 1906 he was elected an Associate of the Linnean Society—an honour and privilege which he always valued highly.

In his work, and, indeed, in his whole life Chadwick was characterized by his meticulous carefulness. Even the slight hesitancy of his speech suggested that he was searching in his mind for the particular word that would convey his meaning most accurately. To him a picturesque exaggeration was a lie, and his hatred of both led him always to the understatement rather than to the overstatement of fact. He never grudged time or trouble to the perfection of detail, and would spend hours on the careful preparation of a label for some specimen or on a business note. The result was a work of art—nothing less would have satisfied him. This side of his character

stands out in the drawings that illustrate his papers. The fine penmanship and accuracy of detail faithfully portray the animals with which he worked. Chadwick drew exactly what he saw, and described the structure in the text.

While naturally of a shy and retiring nature, Chadwick was essentially friendly with his fellow men, and did not readily forget any with whom he had come into contact. His gentle sympathy made him always ready to give help where he could, and the patient friendliness with which year after year he greeted the invasion of students at Easter was nothing short of astonishing.

A man of strict religious principles and strong human affections, he will be remembered by those who knew him as a very gentle, soothing influence amidst the haste and bustle of modern life.

E. C. HERDMAN.

By the death in February 1933 of CARL ERICH CORRENS the Society has lost one of its most distinguished Foreign Members, who, though only elected in 1931, had already shown great personal interest in our proceedings. Born in Munich in 1864, the son of an artist, Correns, in the University of that town, came under the stimulating influence of Prof. Naegeli, an influence which is recognizable in some of his earlier researches dealing with the growth of the cell-wall in some of the Algæ and with the minute structure of vegetable cell-walls in general. In 1892 he established himself as Lecturer (*Privat-Dozent*) in the University of Tübingen, and, though still continuing his investigations into the structure of the cell-wall, he devoted considerable attention to the methods of vegetative reproduction of Mosses, culminating in 1899 in the publication of his '*Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane*'. Attracted also, however, to breeding experiments he discovered, as did also de Vries and Tschermak at the same time, that Gregor Mendel had formulated in 1865 the laws of inheritance, and he showed that these laws were in harmony with modern experimental work. This rediscovery of Mendel's work rivetted his attention to genetics, which throughout his life became the dominating purpose of his investigations. He also published the correspondence between Mendel and Naegeli, whose daughter he had married. His experimental work on the hybridizing of Maize, published in the '*Bibliotheca botanica*', attracted attention, and he was appointed Professor in Leipzig in 1902, and in 1909 was promoted to a Professorship in Münster. When, in 1914, the Kaiser Wilhelm Research Institute for Biology was established, he was appointed its Director, and he held this post, together with a Professorship in the University of Berlin, till his death. Throughout this

period he was untiringly active as an investigator of some of the most difficult problems of inheritance in plants. He devoted a good many of his researches to the solution of the problem of the inheritance of sex, dealing both with dioecious plants, such as *Bryonia* and *Melandrium*, and also with a number of gynodioecious plants. He also investigated experimentally the somewhat anomalous inheritance of variegation in a number of plants, demonstrating that in some cases variegated foliage is inherited through the female parent only. Some of the phenomena of inheritance of variegated foliage led him to the conclusion that the protoplasm as well as the nucleus of the reproductive cells may be concerned in the transmission of certain characters, a subject which he developed in some of his more recent papers. He also made a study of the phenomenon of self-sterility in a number of plants, and, though in his last investigation on *Tolmeia* he had to modify the views put forward with regard to the self-sterility of *Cardamine pratensis*, he considered that further investigations would show that heredity played its part in the development of self-sterility.

Correns was a man of retiring personality. The post he ultimately occupied as head of a research institution was most suited to his tastes, and one in which he could most fruitfully stimulate others. His was the best type of scientific mind; he was interested in the work of others and anxious to be helpful to them. His death from pneumonia at the age of 68 deprives not only Germany of one of its most distinguished men, but botanical science of one of its leading investigators. His eminence was not only recognized in his own country but also in England, and it is gratifying to remember that he was awarded the Darwin Medal of the Royal Society last year for his distinguished researches in genetics.

F. E. WEISS.

By the death of KARL RITTER EBERHARD VON GOEBEL (1855-1932) the Society has lost one of its most distinguished Foreign Members, elected forty-one years ago when he was already one of the leading continental botanists. Two years ago he was awarded the Linnean Medal, and we little thought at the time that his fruitful and active scientific life would so soon be cut short.

Karl Goebel was born in 1855 at Billingham in Baden, where his father was the director of ironworks. Shortly afterwards the family moved to the little town of Winnenden in Württemberg, where Goebel received his earlier education. Later he attended a school in Stuttgart, and when he had passed the 'Landexamen' he was admitted to the Seminary of Blaubeuren, a Grammar School for the education of those

intending to become protestant clergy. In 1873 he entered the University of Tübingen and commenced the study of Theology; but, abandoning the intention of becoming a clergyman, he took up the study of the Natural Sciences, attending the lectures of Hofmeister, under whose stimulating influence he decided to devote himself wholeheartedly to botany.

In 1876 he left for Strassburg, where he graduated and became assistant to de Bary. After a short period of work at the Zoological Station in Naples he went to Würzburg as Assistant to Julius Sachs. In 1880 he became Lecturer (Privat-Dozent) in Würzburg, and after a short teaching period in Leipzig and Strassburg he was appointed to a Professorship in the University of Rostock in 1882. While holding this chair he made his first voyage to the tropics (1885-6), visiting Ceylon and Java. Promoted to the University of Marburg in 1887, he found time to undertake a visit to Venezuela and British Guiana (1890-1), on the return from which he was appointed to the Professorship in Munich, which he held for over forty years. His duties at this larger University were more exacting, and though they involved the remodelling of the Botanical Department and the development of the new Botanical Gardens at Nymphenburg, he was able to continue his travels, visiting Australia and New Zealand (1898), Brazil (1913), and revisiting Java and Sumatra (1924).

Though, as stated above, he came during his studies under the influence of such master minds as Sachs and de Bary, it was the stimulus he had first received from Hofmeister which dominated his botanical activities, and Morphology rather than Physiology or Mycology was the field of research which attracted him and to which throughout his life he devoted his energies. In issuing the fourth edition of his classical 'Lehrbuch der Botanik' Sachs invited him to write the second part, which appeared in 1882 under the title of 'Gründzüge der Systematik und speziellen Pflanzenmorphologie', a translation of which was issued by the Oxford University Press in 1887.

Goebel's extensive travels rivetted his attention on the modifications in the development of the vegetative organs induced by climatic conditions, and his extensive knowledge of these facts he published in the 'Biologische Schilderungen', of which Part I appeared in 1889. In this interesting series, in which he deals with Succulents, Epiphytes, Insectivorous Plants and Water-plants, Goebel showed that in the higher plants at all events adaptation is not direct but is brought about by the influence of surrounding conditions on the meristematic tissues of the growing point. Morphological

and biological studies of lower forms of plant-life, especially of Bryophyta, were published in the 'Buitenzorg Annales'. The more purely theoretical, as distinct from the biological, treatment of Morphology he elaborated later in his masterly 'Organographie der Pflanzen', of which he was able before his death to complete the third edition, and which will always remain a classic. A translation of the first edition was published by the Clarendon Press in 1900. In this masterly treatise, with a wealth of illustrative examples drawn from almost every group of the Archegoniatae and Spermaphyta, testifying to the width of his knowledge, Goebel deals with the form and development of the various organs. But though his treatment embraces so many groups of plants, of which he gives a comparative account, he steers clear of any considerations of the relationship of the various groups. He prefers to deal with ontogenetic facts rather than with phylogenetic speculations. Goebel admits that in dealing with fossil plants, in which developmental processes cannot be studied, morphological investigations may fruitfully lead to phylogenetic considerations. In living plants, however, it is often impossible to determine which are the primitive and which are the degenerate or modified forms. Many phylogenetic problems are, he considered, insoluble with our present knowledge and means of investigation, but definite ontogenetic observations can always be made, and characteristically he defends his point of view with the statement that 'soluble problems seem to me more important than insoluble ones'.

And so he follows in the footsteps of his great master, Hofmeister, pointing out in his admirable biography of the latter that Hofmeister's method had not been phylogenetic or that it assumed a genetic connection between the now-living Cryptogams and Phanerogams. The aim of both in their morphological investigations may be considered to be summed up in the sentence 'es ist ein Bedürfniss des menschlichen Geistes eine Vorstellung sich zu bilden über die Bedingungen der Formgestaltung wachsender Organismen im Allgemeinen'. It was this causal morphology which attracted Goebel more particularly, and in his desire to enlist others in this line of enquiry he published his 'Introduction to the Experimental Morphology of Plants', in the introduction to which he expresses the hopes that the experiments described may be extended by other workers. Goebel's attitude towards morphology and its future extension are most clearly set out in his article on the 'Grundprobleme der heutigen Pflanzenmorphologie' (Biol. Centralbl. vol. xxv, 1905), in which he shows that, while descriptive morphology as an aid to systematic botany may offer little further scope, causal morphology is still in its infancy. The truth of his

statement is evident from the fact that even within the limits of the enlarged third edition of his 'Organographie' Goebel was unable to deal with his continued morphological investigations, and was forced to add two supplementary volumes—'Die Entfaltungsbewegungen der Pflanzen' (1924), and 'Blütenbildung und Sprossgestaltung' (1931). Had he lived to continue his fruitful researches we might have looked forward to further important morphological publications.

Goebel's tall and handsome personality was familiar to many British botanists, for he was a not infrequent visitor to meetings of the British Association. His last visit to England was on the occasion of the International Botanical Congress in Cambridge in 1930. Here, as on all occasions, he showed that kindly disposition which endeared him to all his friends. His last connection with the Linnean Society was in relation to the purchase of the portrait of Julius Sachs, and he expressed his gratification that it had been purchased and presented to the Society by a number of its Fellows.

F. E. WEISS.

JAMES GROVES (1858-1933).—It came as a shock on my return from Bermuda in May to find a request from the Council that I would write an obituary notice of my old friend James Groves. I had not heard of his death, and he appeared in his usual health when I bade him good-bye shortly before leaving England in January.

The brothers Groves were among the earliest of my new friends when I came to the Museum in 1888. I was living near their home in Clapham, where they resided with their mother and sister, and I saw a good deal of them incidentally. Of strikingly different temperament, they were a devoted couple, but Henry, the senior by three years, was the predominant partner. James Britten, who had an amusing knack of labelling folk, dubbed the younger brother the Silent Groves; but, he said, you always felt as if he were waiting in reserve, ready for action if called upon. When James married, Henry felt it as a break in his life, and shortly afterwards followed his brother's example.

James was born in London on 19 January 1858. In 1863 the family removed to Godalming, where the boys attended the local grammar school. In his notice of his brother in the 'Journal of Botany', 1913, James refers to their early life and the development of their interest in Natural History, which began at school. The principal of the school, Peter Churton, was a good general naturalist, and encouraged the pursuit among his elder scholars.

The death of their father in 1869 meant narrowed circumstances and, for the boys, an early entrance into business. The family returned to London, and in 1872, at the age of

fourteen, James entered the office of the Army and Navy Stores, where he worked for forty-six years, retiring, as an Assistant Secretary, in 1918.

Residence in town was not allowed to check the pursuit of Natural History. In the early 'seventies the brothers made the acquaintance of the family of J. E. Sowerby, from whom they borrowed, a volume at a time, the 'English Botany', making drawings or tracings of the plants that they did not know. The Sowerby's also gave them Babington's 'Manual' and other botanical books. Excursions were made to the London commons and other handy places: Wandsworth Common, fifty years ago, was an especially good hunting ground. At that time they were omnivorous collectors, delighting especially in aquatic life.

In 1874 the brothers joined the South London Microscopical Society, then a very flourishing local society, of which Henry later became Hon. Secretary. In this way they made the acquaintance of Robert Braithwaite, then in medical practice in Clapham, Charles Stewart, and Daydon Jackson. Through the exchange columns of 'Science Gossip' they got into correspondence with a number of British botanists, including Mr. T. B. Blow, who is still with us, and who introduced them to Hewett Cottrell Watson, of whom James writes 'we owed much to his help and encouragement'.

In 1874 also they first visited the British Museum, where they met William Carruthers, Henry Trimen and James Britten. The study of the British Roses, begun in 1875, brought an acquaintance with J. G. Baker. Summer holidays between 1873 and 1879 were mostly spent at an uncle's near Southampton, whence trips were made to the New Forest and the Isle of Wight, and notes were collected for Townsend's 'Flora of Hampshire'. Thus together they gained an increasing critical knowledge of the British flora, and meanwhile accumulated a carefully mounted and arranged herbarium. The herbarium was presented to the Department of Botany of the British Museum by James in 1918.

In the course of their work several notable additions were made to the British flora, of which the most striking was *Spartina Townsendi* (Rep. Bot. Exchange Club, 1880), from the mud-flats near Hythe, South Hants, now widely spread on the south coast and of considerable economic importance. Other additions were the hybrid *Ranunculus Hiltonii* (1901), an outcome of their study of aquatic plants, and *Luzula pallescens* (1909).

In 1904 they edited the ninth edition of Babington's 'Manual', revising the nomenclature and bringing the work as much up to date as was possible within the serious limitations imposed by Mrs. Babington. It is to be regretted that

they were not able instead to prepare a new flora on more modern lines. In the above-mentioned notice of his brother James writes, 'we reluctantly undertook the task of editing it within the limitations explained in the preface. We should gladly have left the work in other hands, as we felt that for some time we had been getting out of touch with British botany generally, besides having too little leisure to do the work as it ought to have been done. However, as no one else seemed to be forthcoming, we did the best we could with it'.

It is, however, for their study of the Charophytes that the Groves will best be remembered. They began work on the group in 1877 at W. P. Hiern's suggestion. Prof. Babington helped them with copies of papers and specimens; another helper was Prof. Otto Nordstedt. In the 'Journal of Botany', 1878 (p. 120), they published a short note, '*Chara connivens* in Britain', and in 1880, in the same Journal, a 'Revision of the British Characeae'; followed by a series of 'Notes on British Characeae', which appeared between 1881 and 1898. They collected assiduously, and infinite pains were taken in the preparation and preservation of their specimens. Botanists may remember the beautiful series exhibited by James during the Imperial Botanical Conference in London in 1925. In 1892 James records a visit to Ireland, where they 'enjoyed a positive feast of Characeae in the South and West'. In this year and in 1900 they distributed two fascicles of the British species. In the preparation of the second they were assisted by Canon Bullock-Webster, who continued to work with James after Henry's death in 1912. In 1911 they contributed a monograph of the West Indian Characeae to Prof. Urban's great work the 'Symbolae Antillanae'.

Henry's death, after a long illness in 1912, was an abrupt break of a long and intimate companionship. Though both were married their homes were close together in a quiet road in Clapham. Henceforth James concentrated on the study of the Characeae, British and foreign, and became the recognized authority on the group. In association with the late Clement Reid, and later with Mrs. Reid, he took up the study of the fossil Characeae: a preliminary report on the Charas of the Purbeck Beds appeared in the 'Proceedings of the Royal Society', 1916, and in 1921 he published, again with Reid, a paper on the 'Charophyta of the Lower Headon Beds of Hordle Cliffs' (Quart. Journ. Geol. Soc. lxxvii, pt. 3). During these years Groves was working at his *magnum opus*, the 'Monograph of the British Charophyta', published by the Ray Society in two volumes, issued respectively in 1920 and 1924. In this Canon Bullock-Webster collaborated, while the sister, Mary Groves, drew the beautiful series of

plates which add so much to the value of the work. This was his last important contribution to our knowledge of the British Charophytes, his work on which had extended over nearly fifty years. But he continued to work with unremitting zest, and several publications on extra-European Charophytes appeared in the years that followed :—In our own Journal, 'Charophyta collected by T. B. Blow in Ceylon' (1922), 'Notes on Indian Charophyta' (1924), and 'Charophyta collected by T. B. Blow in Madagascar' (1928); in the 'Journal of Botany', 'On some Indian Charophyta' (with G. O. Allen, 1927), and 'On the Antheridium of *Chara zeylanica*' (1931); and 'New African Charophyta' (with E. L. Stephens) in the 'Transactions of the Royal Society of South Africa' (vol. xiii, 1926).

On his retirement from business in 1918 Groves removed from Clapham to the Isle of Wight, first to Yarmouth, which he found too bleak, and later to Freshwater Bay. His health at the time of his retirement was not good, but as leisure from business brought returning vigour he was wont to miss the society of his botanical confrères and to feel sometimes that he had gone rather far from the centre. He thoroughly enjoyed and made the most of his occasional visits to town, and would bustle into the Herbarium at the Museum or the Linnean Society with a cheerful greeting and a long list of queries to solve. He would talk rapidly, as if there were not a minute to spare, and regretfully decline any suggestion which meant an entrenchment on the short time at his disposal. So I remember him on his last visit, to which I have referred at the beginning of my notice.

James Groves was a good business man, and his knowledge of business and finance, together with his shrewd common sense, were a valuable asset on Councils and Committees. He was an active Fellow of the Linnean Society, which he joined in 1885, and proved a helpful Councillor during the War years of 1914-18. With his brother Henry he was an original member and a Trustee of the South London Botanical Institute, founded by A. O. Hume in 1908, and he continued to take an active interest in its work up to the time of his death. At the Winchester Congress of the South-Eastern Union of Scientific Societies, in 1931, he presided over the Botanical Section, and his address, 'Stoneworts Ancient and Modern', was an excellent popular *résumé* of the position of our knowledge of this group. After making his home in the Isle of Wight he found leisure for local interests. He helped to found the Isle of Wight Natural History and Archaeological Society, and as a staunch conservative played his part in local politics.

Groves was a good friend: a somewhat shy and retiring

exterior veiled a helpful and sympathetic character, ready to put knowledge and experience at the service of a friend. He did not suffer fools gladly, but you knew where you were with him, and his advice was the more valuable on that account. His death on 20 March after a short illness came as an abrupt ending to a long and useful life. The Society has lost a Fellow who had served it well and who took a warm interest in its welfare. And some of us have lost a friend and one on whose experience and discretion we could rely. Our sympathy goes out to his widow and his sister, whose loss is far greater than our own.

A. B. RENDLE.

MALCOLM LAURIE (1866-1932) was born in Edinburgh; he was first educated at the Academy and University there; then followed a visit to Tübingen. A contemporary writes of him as 'a most genial companion and a student of exceptional ability While at Tübingen he became very intimate with Professor Eimer and came into close contact with Professors Vöchting and Georg Klebs'. There, as during his schooldays, his enthusiasm for keeping live animals scattered round him sometimes landed him into household difficulties. In 1899 he went to King's College, Cambridge, after which he worked as a research student under Lankester at University College, London.

In 1894 he was appointed Professor of Biology in St. Mungo's Medical College, Glasgow, and later succeeded A. T. Masterman as extra-mural lecturer at Surgeons' Hall, Edinburgh; there he also taught at the Provincial Training and Heriot-Watt Colleges. These appointments he held until 1918, when he settled in the south of England.

All his days the Pentlands and their fossils had a lasting fascination for him, as shown by various papers between 1894 and 1912. He was an original Member and Founder of the Marine Laboratory at Millport, where he was largely instrumental in starting the educational activities of the Scottish Marine Biological Association. Always interested in live beasts and their ways, a keen observer and a stimulating talker, his companionship ever helped to clear difficulties in the working of the Station. Of many jaunts together, marine and others, I remember best a night spent in a marshy swamp making invisible light (Finsen rays) to attract glow-worms and inaudible noises (Galton whistle) to attract bats.

RICHARD ELMHIRST.

FREDERICK WILLIAM LUCAS (1842-1932), who died at his residence, Speen Court, Newbury, on 13 May 1932, was born at Battersea on 20 July 1842, and was educated at Brighton College. Elder son of Mr. Joseph Lucas, of Stapleton House,

Tooting, solicitor, he became a partner in his father's firm of Messrs. Lucas & Sons, Surrey Street, and afterwards joint partner with his brother.

A man of wide interests and culture, he specialized in zoology, more particularly in mammals and birds, of which he had an extensive knowledge. During his residence in Brighton he added to his existing private museum a large and important osteological collection, which, on leaving the district, he presented to the Brighton Museum. He disposed also of his collections of jade and ivory, some of which are in the Brighton Museum.

Greatly interested in the history of American exploration, his two best-known books are respectively 'Appendiculæ Historicae, or Shreds of History hung on a Horn', published in 1891, and 'Annals of the Voyages of the Brothers Zeni', issued in 1898.

Lucas, although a man of wide knowledge and learning, was of a retiring disposition, and probably few beyond his intimate friends realized his unusual ability and attainments. He would, however, take endless trouble to impart knowledge to those who came to him for help in his own particular, or, indeed, on any other subject.

He was also a musician and an artist—keenly humorous, and of a kindliness that always thought the best.

He was elected a Fellow of this Society in 1905, and was also a Fellow of the Zoological Society and of the American Geographical Society.

I am under obligation to Mrs. Lucas, who has kindly furnished me with most of the information for this notice.

A. BRUCE JACKSON.

Dr. JOHN MASTIN (1865-1932) was the younger son of John Mastin, of Sheffield, and was born at Marchamley, Salop, on 15 October 1865. He died at Pen-y-Groes, North Wales, on 9 July 1932, after a long illness and much suffering.

After some years spent in business, during which time every spare moment was devoted to science and art, he decided to become a painter. Completing his art training at Antwerp, Paris and under Herkomer, in 1898 he started a private school of painting at Sheffield. Many of his pupils became successful painters; and he exhibited his own work at the Royal Academy and elsewhere. As a man of science his interests were very wide, leading him to research work in relation to foods and drugs, and inventions in connection with painting media, waterproof inks and engineering. He was the author of 'The true analysis of milk', 'Parasites of Insects', 'Plate-culture and staining of Amœbæ', as well as several scientific romances.

In 1912 Mastin sent for exhibition at a meeting of our Society two slides of *Polycistina* found on the coast off Whitby, Yorkshire.

In 1901 he married Edith E. Stevenson, who survives him. He was elected a Fellow of the Society on 6 December 1906.

S. SAVAGE.

EDWARD WILLIAM ALFRED AUGUSTINE MAYHEW (? 1855-1933) died at Perth, Western Australia, on 18 January 1933, at the age of seventy-seven. He was elected a Fellow of our Society on 6 December 1888.

Born at Hitchin, Hertfordshire, where his father was a surgeon, he received his pharmaceutical training with a well-known London firm. On account of ill-health he emigrated to New Zealand in 1875, and in the following year went to Western Australia. There he obtained a position as clerk to the superintendent of the Fremantle Prison; but the daily sight of the chain-gang depressed him, and in 1878 he joined the staff of the Western Australian Bank. Later on he became a partner in a chemical business, and was instrumental in starting the first soap works in the State. He claimed to have been the first chemist in Western Australia to engage in the distillation of sandalwood and other essential oils.

Mayhew was the first President of the Pharmaceutical Council of Western Australia, and Registrar of the Council for over thirty years. He was held in high esteem by pharmaceutical authorities throughout Australia; and, to quote Mr. F. P. Gulley, President of the Pharmaceutical Council of Western Australia: 'He was a loyal, diligent and lovable man.'

In 1884 he married Agnes Jewell, and four daughters and three sons survive him.

S. SAVAGE.

Sir DANIEL MORRIS (1844-1933) died at Boscombe on 9 February 1933 in his eighty-ninth year. His outstanding claim to remembrance is as an economic botanist and administrator who initiated and carried through probably the most important agricultural reconstruction that has been undertaken in the British tropical colonies.

Born at Loughor, Glamorgan, in 1844, Daniel Morris was educated at Cheltenham College, and passed to the Royal College of Science, London, and Trinity College, Dublin, where he was later admitted a D.Sc. His official life comprised two long periods of service in the tropics, separated by his tenure of the Assistant-Directorship of Kew under Thiselton-Dyer from 1886-1898. His first appointment was in 1877 as assistant to Dr. Thwaites at Peradeniya, Ceylon, where

for two years his chief work was an investigation of the then prevalent coffee-leaf disease (*Hemileia vastatrix*). His notable West Indian career commenced when he was transferred to Jamaica in 1879 as Director of Public Gardens and Plantations, a post held until his appointment to Kew in 1886. While at Jamaica he visited British Honduras in 1882 and prepared a report which for a generation was the most useful account of the resources of that Colony. The following year a mission to St. Helena resulted in recommendations for the economic development of the island, but unfortunately no action was taken on them. The tropical experience now possessed by Morris proved of great value to him on his appointment as Assistant-Director of Kew, and of no small service to that institution in the part it played in overseas agricultural development. During his twelve years at the Gardens he was engaged in 1890-91 on a special mission to report on the sugar, banana and other industries of the West Indies, and in 1895 he visited the Bahamas in connection with the sisal industry. A turning-point came in the following year, when he was nominated expert adviser on agricultural and botanical questions to the West Indian Royal Commission, appointed during Mr. Joseph Chamberlain's tenure of the Colonial Secretaryship. Following on the recommendations of the Commission Morris proceeded to the West Indies in 1898 as Imperial Commissioner of Agriculture; in this post for ten years he organized and developed the Imperial Department of Agriculture for the West Indies, which proved the industrial salvation of the Leeward and Windward Islands. With the aid of an able staff the sugar industry was vitalized by the improvement of the cane by breeding, the sea-island cotton industry was revived, limbs and cocoa developed and many crop-plants introduced. This work was substantially aided by the regular publication of the 'West Indian Bulletin' and 'Agricultural News' and by the convening of agricultural conferences to discuss progress and future schemes.

On his retirement in 1908 Sir Daniel acted as Scientific Adviser to the Colonial Office, and served on the governing bodies of the John Innes Horticultural Institution and the Imperial Bureaux of Entomology and Mycology. He settled at Bournemouth, became President of the local Natural Science Society, and was President of Section K at the Bournemouth meeting of the British Association in 1919.

Morris wrote much on economic botany. His chief publications include his monographs on fibre-plants ('Kew Bulletin') 'Planting Enterprise in the West Indies' (1883), 'The Colony of British Honduras' (1883), 'Fruit as a Factor in Colonial Commerce' (1887), 'The Colony of the Leeward Islands' (1891), 'Commercial Fibres' (Cantor Lecture, 1895), 'The

Sisal Industry of the Bahamas' (1896), 'Sources of Commercial India-rubber' (Cantor Lecture, 1898), 'Forest Resources of Newfoundland' (1916).

Morris was a keen horticulturist. While at Kew he was treasurer of the Royal Horticultural Society (1888-1891) and played an important part in the developments carried out at Wisley and Westminster. He was a Victoria medallist. He was created C.M.G. in 1893 and K.C.M.G. in 1903. He was elected a Fellow of the Society in 1883. Lady Morris, whom he married in 1879, died in 1932. S. E. CHANDLER.

THOMAS PARKIN was born on 3 February 1845 at Halton Vicarage, Hastings, the youngest son of the Rev. John Parkin, M.A., of Seaton, Cumberland, the first incumbent of the then new parish of Halton. He was educated at Rugby and at Trinity College, Cambridge, taking his B.A. degree in 1868 and proceeding to that of M.A. in 1871. He was called to the Bar of the Inner Temple in 1874, though he never actually practised as a barrister. A man of marked individuality of character, and with sufficient private means to allow him to follow his own inclinations, he soon developed a taste for travel and natural history—especially ornithology.

The winter of 1870-71 was spent by him in Egypt and Nubia in a 'daabayeh' on the Nile. The autumn of 1873 found him on the fells of Norway, shooting and collecting. The winter of 1875-76 was passed in Algeria and the Regency of Tunis. France, Southern Spain, New Orleans, Louisiana and Texas were in due course followed by a trip to the Canaries. His travels may be said to have ended in 1890 with a trip round the world. In that October he sailed to Australia on the last voyage of the fine old clipper ship *Sobraon*, which took 86 days. The captain of the ship gave him special opportunities of collecting albatrosses and petrels, and amongst them he obtained a specimen of the exceedingly rare *Oestrelata incerta*, which is now in the British Museum. From Australia Mr. Parkin went to Tasmania and New Zealand, returning home round Cape Horn and the Brazils. Wide and miscellaneous reading, a real gift for painting and sketching and interest in the bypaths of history and archaeology had all combined to foster his love of travel, whilst his kindly nature and picturesque personality made him a welcome guest in many parts of the world. The impressions made by his travels, therefore, coloured the rest of his life, which was spent at Fairseat, High Wickham, Hastings. Here he rapidly became a well-known figure in the life of East Sussex, a keen shot and cricketer, a local magistrate and committee-man and an active conservative. He was one of the founders of the Hastings and St. Leonards Natural

History Society, for whose journal he often wrote, and for many years he was its president. He showed an equal interest in the literary and artistic interests of the town.

He joined the Linnean Society in 1909. He was also a Fellow of the Zoological, the Royal Geographical and the Royal Historical Societies. He joined the British Ornithologists' Union in 1880, and was made a Vice-President in 1925. As an ornithologist his activities centred in the formation of a large collection of eggs. This in scope was rather unusual, as the egg which he chiefly desired was one with a history to it; so that the collection rapidly became an annotated history of ornithology, recalling the collectors and the expeditions of the past. A few years before his death Mr. Parkin presented his collection, together with the series of registers containing the histories of the eggs, to the Hastings Municipal Museum.

His advanced age had prevented Mr. Parkin from attending the meetings of the Linnean and other societies for some years past, and his own generation has largely vanished; a few, however, will still remember his active kindly spirit and his little Victorian house crammed from attic to basement with books and collections. He died unmarried. H. WHISTLER.

ARTHUR RUFUS SANDERSON (1877-1932) was born at Bradford in 1877. In his early days he was a keen member of the Bradford Natural History Society. In 1916 he contributed a paper to 'The Naturalist' on the minute aquatic 'Fairy-Fly' *Polynema natans*, and in the same year an article on the development of the myxomycete *Brefeldia maxima* Rost. Two years later he published, also in 'The Naturalist', an account of 'The Mycetozoa of the Austwick District'. After being invalided out of the army in the autumn of 1917 he went to Malaya in April 1918, first as pathologist to the Rubber Growers' Association and later as pathologist to the Rubber Research Institute of Malaya. He retained this post, publishing yearly reports of his researches, until in 1931 he returned finally to England. His 'Notes on Malayan Mycetozoa' and a 'Note on the Parasitic Habit of the Plasmodium of *Physarum viride* var. *rigidum* Lister' appeared in 'The Transactions of the British Mycological Society' in 1922. Although he states that his observations were made only at odd moments and at more or less irregular intervals, he gives a valuable record of his experience in collecting Mycetozoa in that moist climate: with his trained eye and persistent enthusiasm he was able to find many species which had not been recorded before from Malaya; his notes on the climate, the habitats and seasonal appearance of the different species, and on the preservation of their

fragile sporangia from the attacks of fungi and insects, are full of interest. His very extensive collection of butterflies and moths has been accepted by the British Museum. He had looked forward with pleasure to naming and classifying the specimens on his return home. He also collected many nests of birds and insects, which the British Museum has acquired.

I am indebted to Mrs. A. R. Sanderson and to Mr. C. A. Cheetham for information regarding Mr. Sanderson's work.

G. LISTER.

Professor JOHANNES SCHMIDT was born on 2 January 1877, and died at Copenhagen on 21 February 1933. By his death at the early age of 56 science loses a man who had achieved much, but who was still doing work of the greatest interest and value, and from whom even more was expected.

Schmidt was especially well known as an oceanographer, and his discovery of the breeding-place of the common eel was a spectacular achievement that made him world-famous. As a young man, however, he did much good work as a botanist, and in recent years, by combining experimental work with biometrical analysis, he had made progress towards the solution of the problems of variation and racial differentiation.

At the University of Copenhagen Schmidt took the degrees of M.Sc. in 1898 and Ph.D. in 1903. From 1902 to 1909 he was biologist to the Danish Commission for Investigation of the Sea, from 1909 a member of the Commission, and from 1927 a representative of Denmark on the International Council for Investigation of the Sea. In 1910 he became Director of the Carlsberg Physiological Laboratory, a post that gave him the opportunity for experimental researches.

In 1899 to 1900 Schmidt accompanied a scientific expedition to Siam, and on his return became editor of the 'Flora of Koh Chang' (1900-16) and author of some of the sections; his work on mangrove-shoots also resulted from this expedition. He published monographs of the Cyanophyceae of Denmark (1899) and of Iceland (1903), described *Richelia*, an alga living in plankton diatoms (1901), and in collaboration with F. Weis produced a large text-book of bacteriology (Copenhagen, 1899-1901; Jena, 1902). From 1904, however, his main work was the investigation of the species and races of fishes, their migrations, times and places of breeding, and larval and post-larval development. At the same time he was attempting, with considerable success, to correlate life-histories and distribution with external factors such as currents, temperature, and salinity. The Atlantic Gadidae, the Plaice, the Argentines, the John Dory and Boar-fish, and the Sun-fishes were among those that he studied. The eel investigation did not differ in method from these

other researches, but because of its difficulty, the persistence required, and the surprising nature of the result, made more appeal to popular imagination. In 1903 and 1904 Schmidt voyaged in the *Thor* to Iceland and the Faroes, and the capture of a larva of the Common Eel at the surface of the sea led him to search for them farther south, with the result that in 1905-1907 he found that full-grown larvae (about 70 mm. long) were abundant at or near the surface over deep water from the Hebrides to Spain. As the *Thor* was unsuitable for work in the Atlantic during the winter the Mediterranean was visited (1908-10), with the expectation that younger larvae would be found there during that season. This expectation was not realized; full-grown larvae were taken in abundance in the summer, but no larvae at all in the winter, and it became clear that the eel did not breed in the Mediterranean and that all the freshwater eels of Europe must go well out in the Atlantic to breed. By 1912 collections made by Danish vessels crossing the Atlantic and a search through the material in the Copenhagen Museum enabled Schmidt to identify a number of larvae from the North Atlantic (some as small as 35 mm. long and from as far west as 53° W.) as larvae of the Common Eel; but it was not until 1920 that he was able to lead an expedition across the Atlantic and to locate the breeding place of the eel as an area S.E. of Bermuda, where alone the earliest larvae, less than 10 mm. long, occurred. The breeding place of the American Eel was found to be a little to the south and west of that of the European Eel, but overlapping it, and larvae of both species were taken together in the Western Atlantic; but it was found that the European Eel, which had to travel a longer distance, had a longer larval history, its elvers being three years old, those of the American Eel only one year old.

The breeding area of the two Atlantic species of *Anguilla* was a place where, at about 500 metres below the surface, the water had a higher temperature and a higher salinity than elsewhere in the Atlantic. Schmidt now studied the Indo-Pacific species, and showed that their distribution depended on the accessibility of breeding areas where like conditions obtained.

Schmidt's principal expeditions were in the *Thor* to the Mediterranean (1908-10), in the *Dana* across the Atlantic to the Caribbean Sea and the Gulf of Panama (1920-21), and again in the *Dana* across the Atlantic, through the Panama Canal to New Zealand, then to the China Sea, Moluccas and Sunda Islands, across the Indian Ocean to the Cape, and so home. This expedition round the world (1928-30) was financed by the Carlsberg Foundation.

These expeditions were planned partly in relation to eel

investigations, but on them numerous hauls were made from the surface down to 3000 metres, obtaining a wealth of material which has not yet been fully studied, but has already greatly advanced knowledge of oceanic life, and particularly the classification, distribution, and development of oceanic organisms, in the reports that have been published under Schmidt's editorship.

From 1913 to 1917 Schmidt made experiments on hops, and published papers on their growth, aroma, and the results of cross-breeding. In 1917 he issued the first of a series of papers that bore the general title 'Racial Investigations'. He first studied the Viviparous Blenny (*Zoarces*), an eel-shaped fish, but, unlike the eel, viviparous, non-migratory, and tending to become localized. Whereas samples of eels from various localities all showed the same average number of vertebrae, *Zoarces* in Danish waters gave different averages for nearly every population examined, the number always decreasing in the inlets, the farther from the open sea the fewer the vertebrae. Year-class analyses and offspring analyses were made and some experimental work was done, the general result being that the number of vertebrae appeared to be hereditary and showed little fluctuation in a population from year to year, but could be slightly influenced by external factors. Experiments were now made on other fishes, and *Lebistes reticulatus*, a little viviparous Cyprinodont, proved particularly interesting, as it was found that the number of fin-rays could be modified by the temperature of the water at the time of early development.

The value of Schmidt's statistical and experimental studies was enhanced by the fact that he knew so well the nature of the problems that he wished to solve. He was fertile in ideas, thorough in his work, and persistent in carrying an investigation through to the end.

Schmidt was elected a Foreign Member of the Linnean Society in 1924, and he received similar honours from many other societies. He was an honorary D.Sc. of Liverpool, and received the Weldon Memorial Prize from Oxford. Among the medals awarded to him were the Darwin Medal (Roy. Soc. London, 1930), the Agassiz Medal (U.S. Nat. Acad. 1930), the Galathea Medal (R. Danish Geogr. Soc. 1930) and the I. Geoffroy St. Hilaire Medal (Soc. d'acclimatation, Paris, 1931). These, and other honours that he received, were no more than the due of a man of such great attainments, who had accomplished so much.

C. TATE REGAN.

BASIL HARRINGTON SOULSBY (1864-1933) was born near Christchurch, New Zealand, and educated at Cheltenham College and at Corpus Christi, Oxford. He also studied at

the Universities of Göttingen and Tübingen, where he acquired a sound knowledge of German and probably also that taste for foreign travel which he retained throughout his life.

In 1892 he entered the British Museum as an Assistant in the Department of Printed Books, and was subsequently put in charge at first of the Map Room and later of the Copyright Office. He was also for a time Deputy Superintendent of the Reading Room.

In 1909 Soulsby was transferred to South Kensington, and on the retirement of Mr. B. B. Woodward in 1921 he was appointed Assistant in charge of the General Library. Here it was his principal duty to continue Woodward's Catalogue of the Natural History Library in five volumes and one supplementary volume, and at the time of Soulsby's death the second supplementary volume, compiled by him, was almost complete.

His most important bibliographical work, however, was the revised second edition of the 'Catalogue of the Works of Linnaeus (and publications more immediately relating thereto) in the Libraries of the British Museum (Bloomsbury) and the British Museum (Natural History)'. Soulsby was at the time of his death seeing through the press the final proofs of this work. A comparison between the size of the two editions may illustrate the vast amount of devoted labour which Soulsby expended on his bibliographical monument. The first edition, prepared by B. B. Woodward and W. R. Wilson for the Linnaeus Bicentenary in 1907, was a modest quarto volume of 27 pages with some 580 entries. The second edition contains over 300 pages with nearly 4,000 entries, and is accompanied by an introduction, full bibliographical notes, plates, and an index. An example of the thorough way in which the work has been performed is seen in the treatment of those difficult items the 'Amoenitates Academicæ'. An analytical account of the ten sets of these dissertations in the Museum Library is followed by a catalogue of the original separate editions, in itself no mean bibliographical exercise.

The scholarly zeal which compiled this catalogue and built up the fine collection of Linnaeana at South Kensington was doubtless fostered by the friendship of Dr. J. M. Hulth, the distinguished Chief Librarian of the Royal University Library of Upsala, whom Soulsby met shortly after his own appointment to the General Library of the Museum. Hulth's celebrated 'Bibliographia Linnaeana' had appeared in 1907, and he placed his immense bibliographical knowledge entirely at his English colleague's disposal, giving him unrestricted access to the magnificent collection at Upsala. Thereafter it became Soulsby's habit to visit nearly every summer the

Scandinavian or Continental Libraries, where his dignified but kindly personality soon won the esteem and respect of the many Librarians whom he met.

Soulsby's *furor bibliographicus* was only equalled by his generosity, for he spent many hundreds of pounds on Linnaean items for the Museum Library, most of them acquired during the compilation of the catalogue. It was a great pleasure to him to be able to present rare and much-wanted books to the Library, and so effectively did he do this that he used to claim that the Linnaean collection at the Museum was 'the most complete after the unrivalled collection at the Royal University Library of Upsala'. It is greatly to be regretted that he did not live to see the fruits of his industry and munificence appear in print, as he looked forward to the publication of the book with just pride and great pleasure.

He was elected a Fellow of the Linnean Society in May 1930 and died 14 January 1933.

A. C. TOWNSEND.

Lt.-Col. JOHN STEPHENSON, C.I.E., F.R.S., was elected Zoological Secretary of the Linnean Society in succession to Dr. G. P. Bidder in May 1930. He died on 2 February 1933. During his brief tenure of office many of our Fellows became aware of his business ability at the Council table and of the wide learning and literary skill that he brought to the editing of our zoological publications, while many more experienced the charm of his personality in the less formal intercourse of the tea-room and the library.

Stephenson was born at Padiham in Lancashire in 1871, and was educated at Burnley Grammar School and at Owens College, Manchester (afterwards the University of Manchester), where he graduated with distinction in Science and in Medicine. After holding hospital appointments in Manchester Royal Infirmary and in the Hospital for Diseases of the Chest in London he competed, in 1895, for the Indian Medical Service, and obtained the first place with a record aggregate of marks for the examination. For the next five years he was on military duty in India, including service with the North-West Frontier Expedition of 1897. There followed a period of plague duty and civil appointments in the Punjab. During all this time Stephenson's interest in Zoology, which had been awakened in Milnes Marshall's class-room in Manchester, had been submerged by the demands of a busy professional life; but in 1906 he was appointed Professor of Biology in Government College, Lahore. There could hardly have been a more fortunate choice for the post. Stephenson quickly showed that he was a born teacher, with the power of communicating to his Indian students something of his own enthusiasm for his subject. Several of his pupils have since earned distinction

by their own researches, and are now holding important positions in various parts of India.

Stephenson's success in winning the respect and confidence of his Indian students, no less than his own wide scholarship, led to his appointment in 1912 to the principalship of the college, and to his being ordered to remain in this post throughout the war instead of reverting to military duty. In 1918 he became Vice-Chancellor of the Punjab University, and on his retirement in 1920 he was created C.I.E.

On returning to this country Stephenson became Lecturer in Zoology in Edinburgh University, and for nine years he was an active member of the important school of zoology which is directed by Prof. Ashworth. Many students who took the higher courses in zoology during that time are very ready to acknowledge the debt they owe to his teaching.

In 1929 Stephenson left Edinburgh and came to live in London. He had just been appointed editor of the 'Fauna of British India' in succession to the late Sir Arthur Shipley, and he was invited to become one of the 'unofficial' scientific staff at the British Museum (Natural History). He was elected to the fellowship of the Royal Society in 1930.

Shortly after going to Lahore, Stephenson had turned his attention to the Oligochaeta, the group of worms which includes the earthworms and their immediate allies. He began by studying the Indian fauna, and later extended his researches to the Oligochaetes of other regions. Nowadays the number of those who are willing to make collections of any group of animals often exceeds the number of those who are willing to study them, and Stephenson, in Edinburgh and in London, found himself asked to report on Oligochaeta from all over the world. Many of these invitations he had to decline, but the collections sent to him provided material for a long series of descriptive memoirs.

The Oligochaeta are one of the groups of animals in which external characters give very little help to the systematist. A study of the internal anatomy by dissection or section-cutting is necessary even for the identification of species, and Stephenson's writings are as much morphological as systematic. Further, he was naturally led to consideration of some of the most fundamental problems of biology. It has long been believed that the earthworms are of peculiar significance to the student of the geographical distribution of animals. Their limited powers of locomotion, the fact that they offer few opportunities for accidental transport and their intolerance of salt water have been held to give them a special value as evidence for the past connections of land-masses now separated by sea. Stephenson considered that the importance of these obstacles to their migration had

sometimes been overestimated, and, above all, he was impressed with the possibility that the occurrence of similar earthworms in distant regions might be due to parallel and independent evolution. Thus, for example, he points out that the former existence of a land-bridge between Australia and India had 'almost become axiomatic in the minds of students of the Oligochaeta'. But he gives reasons for believing that the whole of the earthworm fauna of the world, and particularly that part of it which is common to these two regions, is of recent origin. 'How, on the supposition of a land-bridge, are we to let the Australian earthworms out to India without letting the Asian mammals into Australia?' Stephenson was inclined to believe that the accidental transport of earthworms across 'Wallace's line' was by no means impossible, but he attached even more importance to the possibility that genera apparently identical may have evolved independently in Australia and in India. 'It is, too, in the genera of the Megascolecinae, the group which is common to India and Australia, that we have seen most reason to believe in polyphyletic origins'.

In 1923 Stephenson summed up his studies on the Indian fauna in a volume on Oligochaeta in the 'Fauna of British India', and in 1930 his comprehensive monograph 'The Oligochaeta' was published by the Clarendon Press. This treatise was at once recognized as 'masterly', to use the adjective applied to it by more than one reviewer. It marshals with admirable lucidity a vast mass of facts and handles theoretical questions with wise caution and sound judgment. If Stephenson had written nothing else he would still deserve to be remembered as a great zoologist.

It was characteristic of Stephenson's modesty that he could rarely be persuaded to write or to speak in public on subjects outside his own special field. In November 1931, however, he gave a remarkable address on 'Robert Brown's discovery of the Nucleus in relation to the history of the Cell Theory' at the meeting of our Society which was held to mark the centenary of Brown's discovery. In this address he demolished very effectively the statement universally current in the text-books that 'the Cell Theory was formulated by Schleiden and Schwann in 1839'.

Apart from Zoology Stephenson's interests were many and varied. He was a student of Arabic and Persian literature, and published translations of two old Persian works, one a 14th century treatise on Natural History. He had a fine and discriminating taste in modern as well as in classical literature and the drama. I do not think he had ever cared for any kind of 'sport'. In his later years his week-ends were mostly devoted to long country walks in company

with his wife, usually on the Pentland Hills when they lived in Edinburgh, and on the Chilterns after they came to London.

When all is said and done perhaps the best of Stephenson's work is modestly buried in the writings of those younger zoologists whose researches he directed and whose papers he edited. He had an instinctive sympathy with youth, and his memory is held in affectionate esteem by every student who came under his influence.

Stephenson had suffered for some years from an affection of the heart that could have only one end, and although, as a medical man, he could have no illusions on the subject, he faced it with gallantry and even gaiety, so that his most intimate friends hardly suspected the shadow that hung over his later years.

W. T. CALMAN.

LEONARD GOODHART SUTTON (1863-1932) was the youngest son of Martin Hope Sutton, and grandson of John Sutton who, in 1806, founded in Reading the well-known firm of seed-merchants which bears the family name. He was elected a fellow of the Linnean Society in 1899, and if not a very familiar figure at its meetings it was because his interests were horticultural rather than botanical. For forty-six years he was actively engaged as a member of the firm of which he eventually became senior partner, and was known throughout the world of horticulture, both at home and abroad, as one of the leading exponents of the art and science of gardening. Educated at Wellington College and at the Royal Agricultural College, Cirencester, he continued the study of horticulture in France and Germany, where he gave special attention to seed production and the growing of plants from seeds. It was this aspect of horticulture, in fact, which became his chief interest, and anyone familiar with the Trial Grounds at Reading knows something of the success he achieved in the cultivation of plants raised from seed. Quick to appreciate the ultimate possibilities of a plant, he seems seldom to have failed in the task of evolving and improving new varieties for garden use—witness the range of form and colour in such genera as *Primula*, *Cyclamen*, *Nemesia* and *Cineraria*. Such work does not begin and end merely in the production of new forms that catch the horticultural eye. Years of experiment lie behind the ultimate reward, and Leonard Sutton was fully conscious of the aid which the botanist and the geneticist could bring to the practical problems with which he himself was immediately concerned. To the investigator seeking material for study he gave unstintingly. This recognition of the value of scientific work found expression in his interest in all matters pertaining to education, and for seventeen

years he was chairman of the Reading Education Committee. At the time of his death he was President of the Council of the University of Reading, and to the Departments of Agriculture and Horticulture he was a generous benefactor. In the sphere of Agriculture he played a prominent part as one of the Governors of the Royal Agricultural Society and as Vice-President of the Royal Counties Society.

Sutton was a man of boundless energy, and much of his time and thought were devoted to the municipal life of Reading and to the welfare of the community. He was elected to the Town Council in 1909 and was a member for twenty years. In 1914, soon after the outbreak of war, he became Mayor of the borough, and on two subsequent occasions he held this exacting office. The burden of the war years fell heavily upon him. Of five sons who went to the war four did not return. Such a grievous loss would have broken many a man, but Sutton carried on with steadfast devotion to duty, always mindful of the needs of his fellow men. He was instrumental in raising three companies of Royal Engineers, and for this and for many other public services he received in 1920 the honour of C.B.E. It is no secret that he declined a Knighthood. In 1931 his native town honoured him by making him an Honorary Freeman of the borough, and by general consent no citizen was more worthy of the distinction.

It is not easy to estimate the work which Sutton did for Reading, for his interests and activities were manifold. Much that he did was common knowledge, but throughout his life he went about doing good in that quiet unassuming way which is always difficult to measure. Modesty was the mark of the man. His personal charm was great, and personal relations counted for much. Alert and active, always apparently in a hurry, he accomplished an endless variety of work, yet never failed to give generously of his time to anyone who sought his help or advice. He died suddenly on 13 June 1932 at his home in Reading, and by his death the town has lost one of its most beloved citizens. J. R. MATTHEWS.

M. K. VENKATA RAO (1889-1932) was educated at the High School, Karnool, and the Presidency College, Madras, where he obtained the Palniyandi Gold Medal for proficiency in Botany, and continued post-graduate studies for a year after taking his B.A. degree at the age of seventeen. Here he was the moving spirit of the College Natural Science Association and gained an extensive knowledge of the plant ecology of Madras. Soon afterwards he was appointed Senior Assistant Mycologist in the Mysore Department of Agriculture, a Department in which he served in various capacities until his death. While in government service and busily engaged

in the field-work of the Department he found time to pursue his academic studies, writing a valuable thesis on *Azotobacter* for his M.A. degree in 1912. In 1919 he was awarded the Damodar Das Scholarship for Agriculture, and travelled extensively for some years, taking his Ph.D. at the University of California and M.Sc. at Cambridge. At a later period he visited the Dutch East Indies and elsewhere to gain knowledge to assist him in the laying-out of the Coffee Experimental Station at Balehonnur, under the joint auspices of the Mysore Government and the United Planters' Association of South India.

While still little more than a student he took an active part in organizing and carrying out the campaign against the Koleroga disease of areca-palms due to *Phytophthora Arecae*, which, starting modestly in 1912, has developed into the treatment by spraying of some 2,000,000 palms annually in the Mysore palm-groves. In this uphill task he showed remarkable tenacity of purpose, energy and endurance, though not of robust health. In more recent years he was again engaged in a spraying campaign, this time against coffee diseases, such as the black rot due to *Corticium koleroga* (against which 500 acres were sprayed successfully in 1925) and the leaf disease due to *Hemileia vastatrix*.

As Mycologist to the Department his practical capabilities and versatility had been outstandingly evident, and they led to his employment in the general agricultural activities of the Department—in laying out experimental farms and in appointments successively as Officer-in-Charge of fodder work, as Assistant to the Director of Agriculture and, finally, as Deputy Director of Agriculture.

Outside his official duties he had many interests. He was a member of the State Scout Council and an Assistant Commissioner of Rover Scouts, a capable electrician and engineer, a keen swimmer and a devoted lover of music, in which he had plans for presenting Indian songs in notations on the lines of western music.

E. J. BUTLER.

Although JAMES WALTER WHITE (1846-1932) was elected F.L.S. in 1889 his genial presence was too rarely in evidence at meetings of the Society. Yet by his death on 26 October 1932, at the age of 86, Bristol and the West of England lost its leading phanerogamic botanist and England one of the best of the old school of field-botanists; for White was rarely happier than when collecting and examining plants in the field, either in the British Isles or on the Continent and some of the islands of the Mediterranean.

Born in London 8 August 1846, he went to Dorchester in 1851, and was at school under William Barnes, the Dorset poet.

Leaving school at about fourteen he was apprenticed for five years to Mr. T. B. Groves, pharmaceutical chemist at Weymouth, where he came under the influence of the late W. B. Barrett, the botanist; and he won the medal offered by the Royal Pharmaceutical Society for the best herbarium. Thence he went as an assistant at Allen and Hanbury's, where Daniel Hanbury encouraged him and sometimes invited him to his house at Clapham Common. A few years later he started in business himself at Hampton-on-Thames, and on his twenty-fifth birthday was married to Miss Mary Naldrett, who with their seven sons and four daughters survive him. Mr. and Mrs. White celebrated their diamond wedding in 1931. In 1874 he was invited by a fellow-assistant at Hanbury's to join him in taking over the important chemist's business at Clifton of Giles and Sons, afterwards well known as Giles, Schacht and Co.

Over twenty years ago he was appointed Special Lecturer in Systematic Botany at the University of Bristol, and in 1927 was awarded the Hon. M.Sc. (Bristol). His very fine and extensive herbaria of British and Continental flowering plants and ferns, together with a number of his books, are bequeathed to that University. This addition makes Bristol rank in the matter of herbaria at British Universities probably next in importance to Oxford, Cambridge and Manchester. Many botanists have appreciated his beautifully prepared specimens; and readers of 'The Pharmaceutical Journal' have often enjoyed his racy articles, particularly those descriptive of botanical tours in Spain, the Balearic Isles etc. These tours were usually in the company of his old friend Cedric Bucknall, and once or twice with David Fry or C. E. Salmon.

He joined the Bristol Naturalists' Society in 1878, and was President 1907-09. Notwithstanding an exacting business he early contrived to do much botanical work, particularly in the large area (comprising some 720 square miles) of William Saunders' geological 'Map of the Bristol Coalfields and country adjacent'. His 'Flora of the Bristol Coalfield' appeared in six yearly parts of the 'B.N.S. Proceedings' from 1881, and was published in book form in 1886. In the B.N.S. Jubilee Report, 1913, he wrote 'Fifty Years of Botany in Bristol'. Reference is made there to the Botanical Club founded in 1903 by the late George Brebner. For a number of years this little club held its informal meetings at the house of Mr. White in Woodland Road.

After much further preparation and numerous notes and papers in 'The Journal of Botany' and 'B.N.S. Proc.' White's *magnum opus*, 'The Flora of Bristol', appeared in 1912. In the opinion of many this is one of the best works

of its kind ever published. A long and favourable review by E. S. Marshall in 'Journ. Bot.' 1912 had an additional page by the then editor, because it 'is so admirable an example of how such things should be done'. It excels particularly in its excellent and full introductory matter, the numerous interesting notes under many of the species and the accuracy and care with which habitats (as distinct from localities) are given.

Since 1914 copious supplemental notes and records have been published in 'Journ. Bot.' and the 'B.N.S. Proc.' His last paper on 'The Botany of Bristol', based on his chapter in the British Association 'Handbook', 1898, was written for the Bristol Meeting in 1930, but owing to there being no 'Handbook' that year it was not published until later in 'B.N.S. Proc.' 1931.

Being wisely cautious, and having a sound conception of what should constitute a good species, White gave names to but two or three new plants. *Rubus Bucknalli* was described by him in the 'Journal of Botany', 1899. Another bramble, *R. Naldretti* from Sussex, is now placed as a variety of *R. mutabilis*; and a new and well-marked variety of *Juncus maritimus* from the Scilly Isles he named var. *atlanticus*.

He was for many years an active and valued member of both the British Botanical Exchange Clubs, and contributed to the Herb. Normale, formerly managed by Dörfler at Vienna. From time to time he had been especially interested in Batrachian *Ranunculi*, *Rubus*, *Sorbus* and *Mentha*; but his knowledge of very many European genera was great. White was a prompt and admirable correspondent, and his handwriting was clear and beautiful almost to the end. He was also a good draftsman. After Marshall's death he was President of the Botanical Section of the Somersetshire Archaeological and Nat. Hist. Soc. for three years, 1922-24.

Mr. White's kindness of heart made him ever ready to help other botanists, young and old, and he was always sincere and encouraging. His vivid sense of humour accompanied a dignified and gracious mien. He was buried at Canford Cemetery, Bristol, after a short service at Clifton Parish Church, where he had worshipped for many years.

H. S. THOMPSON.

BENEFACTIONS

LIST *in accordance with Bye-Laws, Chap. XVII. Sect. 1, of all Donations of the amount or value of Twenty pounds and upwards, received during the past Twenty years.*

1913

Royal Society: Grant towards Dr. R. R. Gates's paper on Mutating *Oenotheras*, £60.

Sir Frank Crisp, Bt.: Wallichian Cabinets, £50.

The Trustees of the Percy Sladen Memorial Fund: Second Donation towards the publication of the fifth volume, £200.

1914

Royal Society: Grant towards Miss Gibbs's paper on the Flora of British North Borneo, £50.

Miss Foot: Cost of illustration of her paper on *Euschistus*.

The Trustees of the Percy Sladen Memorial Fund: Third Donation towards the fifth volume, £10.

The same: First Donation towards the sixth volume, £190.

1915

The Trustees of the Percy Sladen Memorial Fund: Second Donation towards the sixth volume, £80.

Miss Foot: Cost of second paper on *Euschistus*, £32 10s.

Royal Society: Donations towards the cost of a paper by Mrs. Arber, D.Sc., £40.

The same: towards paper on Utakwa River plants by Mr. H. N. Ridley, C.M.G., F.R.S., £50.

Miss Marietta Pallis: Instalment of cost of her paper on *Plav*, £30.

Thomas Henry Riches, Esq.: Dr. A. R. Wallace's library on Natural History.

Sir Frank Crisp, Bt.: New shelving for Wallace's Volumes.

1916

Mr. E. Heron-Allen: Contribution to cost of paper on Foraminifera of N.W. Scotland, £44.

Messrs. H. Takeda and C. West: Contribution towards the illustration of their paper, £40.

- Royal Society : Contribution towards the illustration of two papers by Prof. Dendy, £40.
- The same : Contribution towards Mr. Swynnerton's paper on Form and Colouring, £70.
- The High Commissioner for the Union of South Africa, per Dr. J. D. F. Gilchrist, for the illustration of his paper on *Jasus Lalandii*, £30.
- Miss Marietta Pallis : Balance of cost of her paper on Plav, £90 16s. 6d.
- Sir Frank Crisp, Bt. : Phototyped copy of Dioscorides from the 'Codex Anicae Julianae' at Vienna.

1917

- British Ornithologists' Union, etc. : Contribution towards cost of Mr. H. N. Ridley's paper, £20.
- The Royal Society : Second contribution towards the printing of Mr. C. F. M. Swynnerton's paper on Form and Colouring, £75.
- Sir Frank Crisp, Bt. : 'Lindenia', Ghent, 1891-1901. 17 vols. sm. fol.

1919

- Dr. B. Daydon Jackson : MS. index to Linnean Society's Journal, Botany, vols. xxi-xl (1884-1912) and the botanic entries in the 'Proceedings' for the same period.

1920

- The Royal Society : Third contribution towards the printing of Mr. C. F. M. Swynnerton's paper as above, £50.
- The High Commissioner for the Union of South Africa, for the printing of Dr. J. D. F. Gilchrist's paper on *Jasus Lalandii*, Part II, £60.

1921

- The Percy Sladen Memorial Fund : Additional Grant in aid of publication of 'Transactions', 2nd ser., Zoology, vol. xvii, part 4, £72 10s.
- The same : Grant in aid of publication of four papers on the Houtman Abrolhos Islands, £100.
- The Royal Society : Donation in aid of papers by Mr. N. E. Brown and Mr. S. L. Moore, £90.
- Dr. W. Rushton Parker : Donation of a large series of portraits of Naturalists and Persons after whom Genera have been named, and work on rearrangement and annotation of the entire collection.

- Prof. C. S. Sargent, F.M.L.S. : Eight volumes issued by the Arnold Arboretum including 'The Bradley Bibliography'.
- Dr. B. Daydon Jackson : MS. Catalogue of each sheet in the Linnean Herbarium ; bound in two volumes folio.

1922

- The late Sir Joseph Hooker : Donation of his Medals and Decorations. (Reversion to Linnean Society on Lady Hooker's decease.)
- Anonymous donation in aid of publication of the late Dr. E. A. Newell Arber's paper, entitled 'Critical Studies of Coal-Measure Plant-impressions', £60.
- The Percy Sladen Memorial Fund : Cost of printing and illustrating 'Transactions', 2nd ser., Zoology, vol. xviii, pt. 1.

1923

- Dr. W. Rushton Parker : (1) Donation of Oxford New English Dictionary ; vols. i-x, 1888-1928, and Supplement, 1933, 4to. (2) Encyclopædia Britannica : ed. XI, Cambridge, 1920-2. 32 vols. 4to.
- E. Heron-Allen, Esq., F.R.S. : Contribution of £25 towards the cost of paper on the Foraminifera of Lord Howe Island.

1924

- The Percy Sladen Memorial Fund : Cost of printing and illustrating 'Transactions', 2nd ser., Zoology, vol. xviii, pt. 2.

1925

- An Anonymous Donor : New Presidential Chair, emblazoned with the Arms of the Society.

1926

- Subscription portrait of Dr. B. D. Jackson, R.N.O.
- Mr. A. D. Michael : A large number of Books and Pamphlets from his Library.
- The late Mr. A. O. Walker : £200 free of Legacy Duty.
- An Anonymous Donor : £100 to establish a Fellowship in memory of the late Prof. E. A. Minchin, F.R.S., Sec.L.S.
- The Royal Society : Donation in aid of publication of Mr. G. P. Farran's paper on Biscayan Plankton.—Part 14. The Copepoda, £60.

- The late Mr. Frank Morey : £100 free of Legacy Duty.
The late Mr. George Lewis : Books and pamphlets on Entomological subjects.
Capt. E. G. Spencer-Churchill : A copy of a collotype reproduction of 'The herbal of Apuleius Barbarus . . . (MS. Bodley 130)'.
The Percy Sladen Memorial Fund : Cost of printing and illustrating 'Transactions', 2nd ser., Zoology, vol. xix, pt. 1.

1927

- The late Mrs. Mary Anne Stebbing : £100 less Legacy Duty.

1928

- Carnegie United Kingdom Trust : £666 13s. 4d. for purchase of books.
The Royal Society : £160 (£85 in aid of the publication of D. G. Enderlein's paper on 'Die Copeognathen der Seychellen', £75 in aid of Mr. C. V. B. Marquand's paper on 'The Botanical Collections made by Capt. F. Kingdon Ward in the Eastern Himalaya and Tibet in 1924-5').

1929

- Carnegie United Kingdom Trust : £666 13s. 4d. for purchase of books.
The Percy Sladen Memorial Fund : £100 in aid of the publication of papers on the Fauna of the Paraguayan Chaco.
Carnegie Trust for the Universities of Scotland : £28 in aid of the publication of papers on the Fauna of the Paraguayan Chaco.

1930

- Carnegie United Kingdom Trust : £666 13s. 4d. for purchase of books.
An Anonymous Donor : £23 towards the purchase of an Epidiascope.
The Royal Society : £100 in aid of the publication of Mr. H. W. Pugsley's paper 'A revision of the British Euphrasiae' and Dr. T. A. Sprague's paper 'The Herbal of Leonhart Fuchs'.
Mrs. B. Daydon Jackson (the late) : valuable reversion under her Will after three life-tenants shall have died.
Mr. B. B. Woodward (the late) and Mr. A. S. Kennard : a portion of Mr. Woodward's scientific library and reversion of the remainder.

1931

- Miss E. C. Hatchett Jackson : Bust of Charles Hatchett, F.L.S., by Chantrey.
- Major Vivian Seymer : Volumes from the Library of Henry Seymer.
- Exors. of the late Dr. E. J. Bles : Donation in aid of colour collotype plates to illustrate Dr. Karl Peter's paper on *Xenopus laevis*, £100.
- Dr. Francis Pierrepont Barnard : Bequest of Sir James E. Smith's seal, his collection of seal impressions, and some portraits.

1932

- Mr. Francis Druce : Donation towards the cost of new books, £50.
- The Royal Society : Donation in aid of the publication of papers resulting from Dr. Worthington's Expedition to the East African Lakes, £75.
- Subscription portrait of the late Professor Julius von Sachs, F.M.L.S.
- Cambridge Expedition to the East African Lakes, 1930-31 (Dr. E. B. Worthington, leader).—Unexpended balance of expedition funds, for the publication of the scientific results, £175.
- Carnegie Institution of Washington : Donation of a considerable number of its publications.

1933

- The Royal Society : Donation in aid of the publication of Dr. H. Boschma's paper 'The Rhizocephala in the collection of the British Museum', £60.

TREASURER'S ACCOUNTS FOR THE

(Presented at the Anniversary

*Receipts and Payments of the Linnean Society***General**

	RECEIPTS	£	s.	d.	£	s.	d.
To Balance at 1 May 1932		543	17	11			
„ Cash in hand		12	2	7			
					556	0	6
„ Admission Fees					44	0	0
„ Arrears of Annual Contributions		40	0	0			
„ Annual Contributions for year		2420	0	0			
Do. in advance		89	0	0			
					2549	0	0
„ Interest on Investments (including Income Tax recovered)					304	9	2
Do. Deposit					11	18	10
„ Sales of Publications:—							
Transactions		65	9	3			
Journals		207	16	5			
Proceedings		12	11	1			
Library Catalogue		1	8	9			
					287	5	6
„ Donations in aid of Publications					256	0	0
„ Donations for General Purposes					51	0	0
„ Miscellaneous Receipts					37	3	0
					£4096	17	0

Library

	RECEIPTS	£	s.	d.
To Balance 1 May 1932		7	8	10
„ Interest on Investments (including Income Tax recovered)		49	14	10
„ Transferred from General Account		550	0	0
		£607	3	8

Fellows' Postal

	£	s.	d.
To Balance at 1 May 1932	60	12	7
„ Deposits during year	11	14	9
	£72	7	4

YEAR ENDED 30 APRIL 1933

Meeting, 24 May 1933.)

*from 1 May 1932 to 30 April 1933.***Account**

PAYMENTS	£	s.	d.	£	s.	d.
By Coal, Electric Current, and Gas.....	87	9	7			
„ Furniture.....	9	5	11			
„ Repairs : Sundry	18	10	8			
„ Taxes and Insurance	62	5	6			
„ Miscellaneous Printing and Stationery.....	159	5	7			
„ Petty Expenses (including Tea and Postage)	183	5	5			
„ Publications :—						
Printing	950	15	9			
Illustrations.....	158	10	0			
Distribution.....	67	1	2			
				1176	6	11
„ Salaries and Wages, etc.				1086	0	0
„ Transferred to Library Account				550	0	0
„ Zoological Record : Donation for 1932 volume				15	0	0
„ Purchase of £98 10s. 2d. 3½ per cent. Conversion Stock (Staff Pension Fund)				100	0	0
„ Linnean Medal				14	10	0
„ Balance at 30 April 1933	622	0	10			
„ Cash in hand.....	12	16	7			
				634	17	5
				<u>£4096</u>	<u>17</u>	<u>0</u>

Account

PAYMENTS	£	s.	d.
By Books	31	10	9
„ Periodicals.....	437	17	10
„ Binding	71	11	0
„ Balance at 30 April 1933	66	4	1
	<u>£607</u>	<u>3</u>	<u>8</u>

Account

	£	s.	d.
By Postage during year.....	9	17	4
„ Balance at 30 April 1933	62	10	0
	<u>£72</u>	<u>7</u>	<u>4</u>

Separate Account

	£	s.	d.		£	s.	d.
To Balance at 1 May 1932 :—				By Goodenough Fund :—			
Westwood Fund		£72	5 10	Transferred to Annual Contributions...		8	0 0
Trail Award Fund		7	11 8	Hooker Lecture Fund :—			
Crisp Award Fund		39	4 7	Award and Expenses to Lecturer		31	10 0
Hooker Lecture Fund		112	12 8	Minchin Fellowship Fund :—			
Goodenough Fund		23	15 8	Transferred to Annual Contributions...		4	0 0
Linnean History Fund		21	9 6	Staff Pension Fund :—			
Minchin Fellowship Fund ..		3	5 0	Purchase of £20 13s. 10d. 3½ per cent.		20	15 10
				Conversion Stock			
Westwood Fund :—				Westwood Fund :—			
Proceeds of Sale of £50 4 per cent.				Purchase of £61 17s. 11d. India 3½ per		54	17 9
Victory Bond				cent. Stock			
Goodenough Fund :—				Goodenough Fund :—			
Proceeds of Sale of £100 4 per cent.				Purchase of £123 15s. 11d. India 3½ per		109	15 6
Victory Bonds				cent. Stock			
Hooker Fund :—				Hooker Fund :—			
Proceeds of Sale of £50 4 per cent.				Purchase of £61 18s. 0d. India 3½ per		54	17 9
Victory Bond				cent. Stock			
Interest on Investments (including				Balance at 30 April 1933 :—			
Income Tax recovered) :—				Westwood Fund		£81	18 2
Westwood Fund		£9	12 4	Trail Award Fund		11	1 8
Trail Award Fund		3	10 0	Crisp Award Fund		46	14 7
Crisp Award Fund		7	10 0	Hooker Lecture Fund		103	11 6
Hooker Lecture Fund		22	8 10	Goodenough Fund		24	0 10
Goodenough Fund		8	5 2	Linnean History Fund		21	9 6
Minchin Fellowship Fund ..		5	0 0	Minchin Fellowship Fund ..		4	5 0
Staff Pension Fund		20	15 10				
						293	1 3
						£576	18 1

Market Value.
30 April 1933.

General Account

£	s.	d.
1000	0	0
1200	0	0
1000	0	0
1000	0	0
1000	0	0
312	0	0
3296	0	0
Metropolitan 3 per cent. Stock 1941	@102	1020 0 0
India 3 per cent. Stock	@ 74½	894 0 0
Eastern Bengal Railway 4 per cent. Irredeemable Debenture Stock	@ 92½	925 0 0
Great Western Railway 4 per cent. Debenture Stock	@102½	1025 0 0
London Midland & Scottish Railway 4 per cent. Preference Stock	@ 37½	117 0 0
4½ per cent. Conversion Stock 1940-44	@111½	3675 0 10

Library Account

£	s.	d.
450	0	0
200	0	0
530	0	0
88	9	8
Forth Bridge Railway 4 per cent. Stock (Bentham Bequest)	@ 95	427 10 0
4½ per cent. Conversion Stock 1940-44 (Walker and Morey Bequests)	@111½	223 0 0
East Indian Railway 3½ per cent. Debenture Stock (Tagart Bequest)	@ 81	429 6 0
London County 5 per cent. Stock 1940-60 (Stebbing Bequest)	@ 112	99 2 0
	£7656	0 10

Separate Account

£	s.	d.
£1012	9	5
232	5	0
638	4	5
142	0	0
100	0	0
300	0	0
61	17	11
61	18	0
123	15	11
100	0	0
705	19	1
Metropolitan Water Board 3 per cent. "B" Stock (Westwood Fund)	@ 90	1178 18 0
Ditto	@ 90	209 0 6
Ditto	@ 90	574 7 11
New South Wales 3½ per cent. Stock, 1930-50 (Trail Award Fund)	@ 90	127 16 0
2½ per cent. Consolidated Stock (Crisp Award Fund)	@ 96	96 0 0
India 3½ per cent. Stock (Westwood Fund)	@ 75½	226 10 0
Ditto	@ 86½	53 10 10
Ditto	@ 86½	53 10 10
Ditto	@ 86½	107 1 8
London County 5 per cent. Stock 1940-60 (Minchin Fellowship Fund)	@112	112 0 0
3½ per cent. Conversion Stock (Staff Pension Fund)	@ 101	713 0 3
£7 17s. 2d. Ditto, to be transferred on 1 May 1933.		£2272 18 0

FRANCIS DRUCE, *Treasurer.*

We have (in conjunction with the Professional Auditor, who certifies as to all details) audited the Accounts of the Society for the year ended 30 April 1933, and found them correct. We have verified the Investments and Bank Balances.

Dated this 9 May 1933.

W. B. KEEN, *Chartered Accountant.*

Auditors.
F. E. WEISS,
J. RAMSBOTTOM,
D. J. SCOURFIELD,
H. W. PUGSLEY,
ELSIE M. WAKEFIELD,
J. R. NORMAN,

ADDITIONS AND DONATIONS

TO THE

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1932-33

Note.—Separate copies of papers which are included in periodicals received by the Library are no longer catalogued. Names of donors are given in square brackets.

All publications of the Carnegie Institution of Washington catalogued below have been presented by that Institution.

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[*Continued as*]

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Objects, equipment and methods. By S. KEMP, A. C. HARDY, and N. A. MACKINTOSH. Pp. 141-232.

The Natural History of the Elephant Seal, with notes on other seals found at South Georgia. By L. HARRISON MATTHEWS. Pp. 233-256.

Southern Blue and Fin Whales. By N. A. MACKINTOSH. Pp. 257-540.

Parasitic Nematoda and Acanthocephala collected in 1925-1927. By H. A. BAYLIS. Pp. 541-560.

The Birds of South Georgia. By L. HARRISON MATTHEWS. Pp. 561-592.

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Thoracic Cirripedes collected in 1925-27. By C. A. NILSSON-CANTELL. Pp. 223-260.

Oceanic Fishes and Flatfishes collected in 1925-27. By J. R. NORMAN. Pp. 261-370.

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The age of Fin Whales at physical maturity, with a note on multiple ovulations. By J. F. G. WHEELER. Pp. 403-434.

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Oligochaeta.—Part II. Earthworms. By GRACE E. PICKFORD. Pp. 265-290.

Foraminifera.—Part I. The Ice-free Area of the Falkland Islands and adjacent seas. By EDWARD HERON-ALLEN and ARTHUR EARLAND. Pp. 291-460.

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